PHYTOLITH ANALYSIS AS A PALEOECOLOGICAL PROXY WHEN EXAMINING BISON ANATOMICAL AND BEHAVIORAL CHANGES IN THE GREAT PLAINS

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Abstract: The demise of mammoths, during the terminal Pleistocene extinction event, thrust bison into a role as both the keystone herbivore of the Great Plains grasslands and the most important prey resource for the established human populations. Since the end of the Pleistocene, the genus Bison underwent significant anatomical and behavioral changes. This study examines opal phytoliths embedded in dental calculus of prehistoric bison specimens as a proxy for reconstructing environmental context of anatomical and behavioral changes underwent by the Great Plains bison since the terminal Pleistocene. The strategy includes comparing prehistoric phytolith assemblages with those of modern bison in various types of grasslands. The paleo-bison examined were sourced from the Beaver River Bison Hunting Complex, the Ravenscroft II Bison Kill Site and the Folsom Site, in Oklahoma and New Mexico. This research shows that phytolith analysis is a viable method of adding additional data to other studies on bison paleo-ecology. The phytolith counts obtained indicate a significant climatic and potential ecological difference between the ancient bison and the modern references, which were analyzed.

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I. INTRODUCTION

Problem statement:

One of the largest gaps in humankinds' combined knowledge is our planet's environmental history. The further we look back in time, especially pre-written record, the less we know. Thus, our knowledge of the prehistoric past must rely on what little physical information is available in the fossil record and from proxy values obtained from these discoveries.

In North America, bison have been the keystone herbivore in the Plains region since the disappearance of the mammoths at the end Pleistocene extinction event. The extinction of the largest herbivores thrust bison into a role as both the managers of a changing environmental landscape and as the main animal resource for the established human populations of North America (Graves 2008). Despite their obvious importance, remains a poor understanding of the ecological and behavioral characteristics of ancient bison populations after the last glaciation.

During the time between the last Ice Age and the present, the literature shows that the genus *Bison*, underwent significant physical and behavioral changes (Wyckoff and Dalquest 1997; Rivers, Solounias and Mihlbacher 2007; Hill, Hill and Widga 2008). The physical changes, which are obvious from skeletal remains illustrate that bison became much smaller over time. This diminution should correspond with some external force and may have accompanied a change in behavior.

Although animal behavioral changes are difficult to determine from the fossil record, it is possible to use proxy data, such as stable isotopes, which suggests dietary patterns and potential movements across the landscape (Wyckoff and Dalquest 1997; Rivers, Solounias and Mihlbacher 2007; Widga, Walker and Stockli 2010). To this approach, the analysis of grass phytoliths may also add some important clues to the physical and behavioral changes bison underwent, as grasses constitute the bison's main food source (Knapp et al. 1999; Boyd 2003). Thus, this study tests the viability of silica phytolith analysis as a proxy to bison feeding behavior, which may have had consequences in the progression of bison diminution during the early Holocene.

This research will study phytoliths obtained from dental calculus of bison specimens, both modern and ancient. The results obtained should be evaluated in the context of other studies of bison diminution on the Great Plains as a supplemental approach to other more established methodologies such as isotope fractionation (Widga, Walker and Stockli 2010; Carlson et al. 2018). This study will be useful to other scientists in this field looking to apply alternative methodologies.

Conceptual background of this research:

American bison and its diminution:

Bison inherited an increased ecological importance after the terminal Pleistocene extinction (Wyckoff and Dalquest 1997; Knapp 1999; Boyd 2003). Secondly, bison are a

common species whose archaeological remains are available. Bison remains are common in the Great Plains as they served as the primary protein source for the humans from the end of the Pleistocene to the modern era (Wyckoff and Dalquest 1997). Bison also serve as the keystone herbivore for the natural Great Plains environment; their behavior and diet are integral to shaping this ecoregion through time (Wyckoff and Dalquest 1997; Knapp et al 1999; Boyd 2003). Bison are also obligate grazers, feeding on grasses, which are the dominant producers of phytoliths within this ecosystem (Knapp et al 1999; Boyd 2003). This trifecta of traits; availability, ecological importance, and copious grass consumption make bison an ideal animal for this type of study.

Not all of the bison included within this study are of the modern type. The species under consideration are *Bison antiquus* or *Bison occidentalus* from the prehistoric sites (Bement 1999; Meltzer 2006), and *Bison bison* from the modern sites. One important distinction between these species is size, *Bison antiquus* was a much larger animal than the modern *Bison bison*. Both taller and heavier built, the average *Bison antiquus* would have weighed 802 ± 183 kg (Martin, Mead and Barboza 2018), roughly twice what a modern bison would (479 ± 177 kg) (Martin, Mead and Barboza 2018) and have been 25% taller at the shoulder in an average individual (Lewis et al 2010; McDonald 1981; Hay 1913). These estimations are based on measurements made of skulls,metacarpals and calcaneum (Martin, Mead and Barboza 2018; Lewis et al 2010; McDonald 1981; Hay 1913). The intermediate form was similar in outward appearance to both *B. antiquus* and *B. bison* but was smaller than *B. antiquus* and larger than the modern *B. bison* (McDonald 1981; Martin, Mead and Barboza 2018). It is important to

remember however, that extremely large members of *Bison bison* would be within the normal size range for *B. antiquus* (Lewis et al 2010; Martin, Mead and Barboza 2018). Other than size, the physical differences between the species are minimal, as *B. antiquus* is the immediate ancestor to the more familiar *B. bison*. There is also evidence that *B. antiquus* may have behaved differently from the younger *B. bison* as it appears to not have congregated in as large of herds as were commonplace in pre-western expansion America, which commonly numbered in the hundreds of thousands or more (Wilson 1978; Shaw 1995).

Diminution is defined in the literature as when a species' body size reduces over time (Hill, Hill and Widga 2008; Lyman 2004). This occurred during the late Pleistocene into the eraly Holocene when bison evolved from the giant long-horned bison, *Bison latifrons* to the modern *Bison bison*. There is still debate on the underlying reason and mechanisms for diminution (Lyman 2004; Lewis et al. 2010; Hill, Hill and Widga 2008; Faith 2011). There are however, some widely accepted facts; we know floral composition of the Great Plains changed in the few thousand years after the last Glacial Maximum (Fredlund and Tieszen 1997; Woodburn et al. 2016). The climate went from being cold and wet, to warmer and wet, to cool and dry, to warm and dry and this brought adjustments in grassland composition changing from a C_3 dominated system to a C_4 dominated system in some regions (Fredlund and Tieszen 1997; Woodburn et al. 2016). We also know that Bison were the predominant prey species of the humans occupying the area after the end-Pleistocene extinction (Graves 2008; Bement 1999). We know that Bison as a genus were incredibly prominent animals often shaping the landscape around them and

that bison have suffered in recent history due to human impact (Gates et al. 2010; Boyd 2003; Knapp et al. 1999).

The literature is divided over the underlying causes of diminutions in the genus over time (Lyman 2004; Lewis et al. 2010; Hill, Hill and Widga 2008; Faith 2011). The two prevailing theories, are human caused diminution (Hill, Hill and Widga 2008), and diminution driven by changing grassland composition due to climate change (Lewis et al. 2010; Lyman 2004; Faith 2011; Hill, Hill and Widga 2008).

Phytolith analysis:

Another facet of this research is plant phytoliths and phytolith analysis. First discovered by the German microbiologist Christian Ehrenberg in 1835, plant phytoliths, also called opal phytoliths in the literature, are intracellular silica deposits inside the cell structure deposited by some species of plants (Piperno 2006; Fredlund 2001). Phytoliths were first observed in the 1840s and formed a significant part of the soil samples collected by Darwin on the Beagle, however their study was only popularized internationally in the 1950s with most previous study being done solely in Germany (Fredlund 2001).

There are sixteen distinct morphologies of phytolith used in this study. These can be broken into two larger groups, the short cell phytoliths and the long cell phytoliths (Piperno 2006). The first type of long cell phytoliths are the trichomes. These phytoliths are aciculate in shape and appear to look like thorns or spines under a microscope, the literature theorizes that trichomes are used by the plant for protection purposes (Piperno 2006). The literature states that the aciculate form may help protect against predation from micro-herbivores or from

pathogenic fungi (Piperno 2006; Thorn 2007). These phytoliths display diverse morphology (Piperno 2006).

The other two types of long cell phytolith are the elongate and bulliform phytoliths. The literature suggests that these morphologies exist to aid in the plant's structural integrity by providing rigid support within otherwise softer structures (Piperno 2006; Thorn 2007). Beyond protection and structure, the physiological function of many types of phytoliths that plants produce is not well understood (Piperno 2006; Thorn 2007). These remaining types are still vital to researchers because they include the diagnostic phytoliths. The diagnostic phytoliths, called short-cell phytoliths by the literature, come in too many morphotypes to enumerate in this document (Piperno 2006). However, they are vital within the context of this research because they can be identified via light microscope down to the subfamily level, sometimes even to lower taxonomic ranks (Piperno 2006).

Plants create phytoliths in their tissues from the silica suspended in the groundwater they absorb. The plants then use the water for photosynthesis and respiration, leaving the silica behind. The type, number and location of these phytoliths are genetically and environmentally influenced (Piperno 2006). Some plants form lots of phytoliths, such as grasses, some form only a few, like the sedges, while some others, such as most deciduous trees, form no phytoliths at all (Piperno 2006). The type of tissues in which silica phytoliths are deposited is also genetically influenced, with some species having phytoliths within some plant structures, but not in others. In general, the literature observes that reproductive structures have higher occurrence levels of phytoliths than do photosynthetic or support based structures

(Piperno 2006). Phytoliths also accumulate as a plant ages, with older plants having more phytoliths than younger plants (Piperno 2006).

Phytoliths can be advantageous over other proxy measurements because of their durability and diagnostic properties (Stromberg et al 2018). When a plant dies, all the phytoliths that the plant contains are deposited on the ground (Piperno 2006; Fredlund 2001). The plant rots away and the phytoliths are left behind, undamaged due to their non-biologic siliceous makeup. The phytoliths then leave a diagnosable fingerprint in a soil series (Stromberg et al. 2018).

In the literature, the durability of phytoliths is quite evident, they are resistant to dissolution in water and even weak acids, they are unharmed by weather effects and can endure millennia given good circumstances (Thorn 2007). Many times, researchers are examining phytoliths from the Pleistocene, which are tens of thousands of years old (Cordova and Agenbroad 2009; Fredlund and Tieszen 1997; Gobetz and Bozarth 2001, Bement et al 2007; Stromberg et al. 2018), but there are examples of surviving phytoliths in samples much older. For example, phytoliths were discovered in sauropod coprolites from the Maastrichtian age, roughly 70 million years ago. Surviving the physical and chemical digestion of a dinosaur digestive tract as well as surviving fossilization is a testament to phytolith durability (Thorn 2007; Stromberg et al. 2018). Of course, the fossilization process destroys far more phytoliths than survive it and finding phytoliths in a sample that old is an anomaly, but phytoliths can still be a dependable way to identify the original flora at an ancient study locale (Fredlund 2001).

Phytoliths provide an effective proxy measurement for paleo-biological examinations further back in time than some other methodologies (Fredlund 2001).

Phytolith Indices:

When utilizing phytolith analysis many researchers use established indices to further gain insight into their samples. Researchers use phytolith indices to estimate diverse conditions such as tropical tree canopy cover or aridity (Bremond et al. 2008). In this study, two indices are used. The first index is the humidity-aridity or the I_{ph} index. The I_{ph} index relies on the relative abundances of C_4 phytoliths produced by the Chloridoideae family of short grasses compared to the sum of the Chloridoideae and Panicoideae (C_4, tall grass) phytoliths (Nogué et al 2017). It is calculated by taking the abundance of the short saddle morphotype divided by the sum of the short saddles added to the Panicoid bilobates, the crosses and the polylobates (Nogué et al 2017). Chloridoid grasses grow well in dry conditions while the Panicoid grasses are more typical of the tallgrass prairie, which flourishes in comparatively wetter conditions (Nogué et al 2017). What this means is that a high value, approaching one, indicates dry climatic conditions. A lower comparative value would indicate wetter conditions (Nogué et al 2017). There are some issues with this regarding using dental samples as dental samples are only indicative of what was consumed, and bison consumption may not be equal across the landscape. Thus, it will be important to only use the values generated in a comparative capacity against the other dental samples.

The second index I will be using is the I_c, or climatic index. Twiss defined this index as the ratio of Pooideae phytoliths (C_3) compared to the sum of the Pooideae, Panicoidea and

Chloridoideae phytoliths (Twiss 1987, Twiss 1992, Barboni Bonnefille Alexandre and Meunier 1999). This index is used to show the estimated proportion of C_3 grasses, which can then be used to suggest prevailing climatic conditions (Barboni, Bonnefille, Alexandre and Meunier 1999). Thusly a higher value for the I_c index indicates a cooler climate, whereas a lower value indicates a locale with few cool season grasses and higher prevailing temperatures. Again, it is important to remember that this study is restricted to dental phytolith values for many of these measurements. This means that values obtained will not be compared to the soil values but instead to the modern dental values in the study. Bison migration may further obfuscate any results obtained, as the sample would be drawn from a larger geographical area, potentially spanning several climatic zones.

Phytolith soil analysis:

In phytolith soil analysis, researchers from the literature take samples from available soil series and process them for phytoliths. Once the assemblage is obtained and diagnosed, it can be used to generate an accurate phytolith bearing floral assemblage (Cordova et al 2011; Cordova and Avery 2017; Gobetz and Bozarth 2001; Woodburn et al. 2016). This means that with an intact soil series it is possible to track the changes in flora over time by examining the phytoliths present in the different layers (Cordova et al 2011; Cordova and Avery 2017; Gobetz and Bozarth 2001; Woodburn et al. 2016). It is important to remember that this methodology is limited in the regard that not all plants are phytolith bearing and thus cannot deposit phytoliths within the soil during decay of the biological material (Cordova et al 2011; Cordova

and Avery 2017; Gobetz and Bozarth 2001; Woodburn et al. 2016). Since this study is focused on grasslands, this issue is circumvented, as the grass families in the Great Plains are phytolith bearing (Piperno 2006; Stromberg et al 2018).

From these reconstructed floral assemblages, it is possible to infer more data such as prevailing temperature and the amount of precipitation available in that particular place and time (Pokines et al. 2019; Stromberg et al. 2018; Woodburn et al. 2016). This is possible since environmental niches are limited by climatic conditions (Metcalf et al 2014). This inferred paleoclimatic data is a requirement to construct a full idea of what is happening biogeographically. Thus, Metcalf et al. (2014) used a multidisciplinary approach to test the alternative hypotheses of paleo-bison population distributional biogeography. They used spatial-temporal fossil data, ancient DNA sources, paleo-climate reconstructions, niche envelope models and coalescence modelling to create models predicting the significant factors concerning bison distribution. What they found in the models was that the paleoclimate data was the most influential factor to determine bison distribution right up until the increase in hunting due to firearms (Metcalf et al. 2014). Unfortunately, they did not include phytolith analysis in this study, probably due to the unavailability of data. These results can be extrapolated to many situations were paleoclimate can be used to predict faunal presence or absence with acceptable accuracy.

Soil phytolith analysis can provide us with this vital climatic data. However, it is imperative to remember that it is not without faults. Researchers know this and thus shape their questions within the limitations of this type of analysis. First, phytoliths obtained from soil

horizons in sedimentary sequences cannot be considered a localized record. This is due to phytolith translocation (Piperno 2006; Stromberg 2018; Fredlund 2001). The most common types of phytolith translocation are through physical phenomenon including wind, fire, water or faunal transference (Stromberg 2018; Fredlund 2001). These forces can transport the plant detritus that phytoliths originate from, or the phytoliths already contained within the soils. This decreases the spatial accuracy, so researchers treat phytolith data as local or regional data rather than site specific (Pokines et al. 2019; Fredlund and Tieszen 1997; Cordova et al. 2011). Secondly, phytoliths can be translocated within the soil profile, from upper layers to lower lying ones due to the action of groundwater or bioturbation (Pokines et al. 2019; Fredlund and Tieszen 1997; Cordova et al. 2011). This means that phytoliths deposited in one time may be transported to other horizons, which represent different eras.

Phytolith Dental Analysis:

Completing analysis on dental samples from herbivores is possible as phytoliths can become deposited in the tooth calculus accretions, colloquially known as plaque (Pokines et al. 2019; Middleton and Rovner 1994; Gobetz and Bozarth 2001; Cordova and Avery 2017; Bozarth and Hofman 1998; Armitage 1975). When herbivores feed, they consume plants that contain phytoliths and there is a chance that some of these phytoliths become embedded in the calculus buildup on the teeth during mastication (Fig. 1). This calculus can then be extracted post mortem and processed so that the phytoliths can be examined, diagnosed, and counted. The researchers in the literature then use these counts to determine the diet of the individual

herbivore (Pokines et al. 2019; Middleton and Rovner 1994; Gobetz and Bozarth 2001; Cordova and Avery 2017; Bozarth and Hofman 1998).

Once diet is determined, it is possible to use these values in conjunction with associated soil assemblages to hypothesize about an individual's ecological context. Practically, this means that if we know where an animal was living, what type of plants lived there, and what the animal's diet was, researchers can use that data to form hypotheses about the behavior of that individual (Gobetz and Bozarth 2001). It also may be possible to determine generalized migration patterns of individuals if the observed phytoliths from tooth calculus does not match what is found from soil phytoliths at the kill site. When taking soil samples for this comparison, it is necessary to obtain the sample away from the kill site as the immediate soils may be contaminated, as phytoliths are common within the rumens of ungulates (Rovner 1983).

Dental calculus sampling is not without its drawbacks. One of the drawbacks is that because deposition occurs under such specific circumstances and calculus buildup continues throughout the lifespan of an individual, dental phytolith assemblages is not a snapshot of the last meal (Stromberg et al 2018). Rather dental calculus contains a record of diet over an entire lifespan (Stromberg et al 2018; Middleton and Rovner 1994; Fredlund 2001; Cordova and Agenbroad 2009). An older individual will have more calculus than a younger one as well as correspondingly more embedded phytoliths due to the cumulative nature of phytolith deposition (Stromberg et al 2018). Therefore, it is possible to use calculus data as a mean dietary intake value (Gobetz and Bozarth 2001). Clearly, this method is only viable on

herbivores, and is especially applicable for herbivores that predominantly feed on grasses and other diagnostic phytolith producing plants.

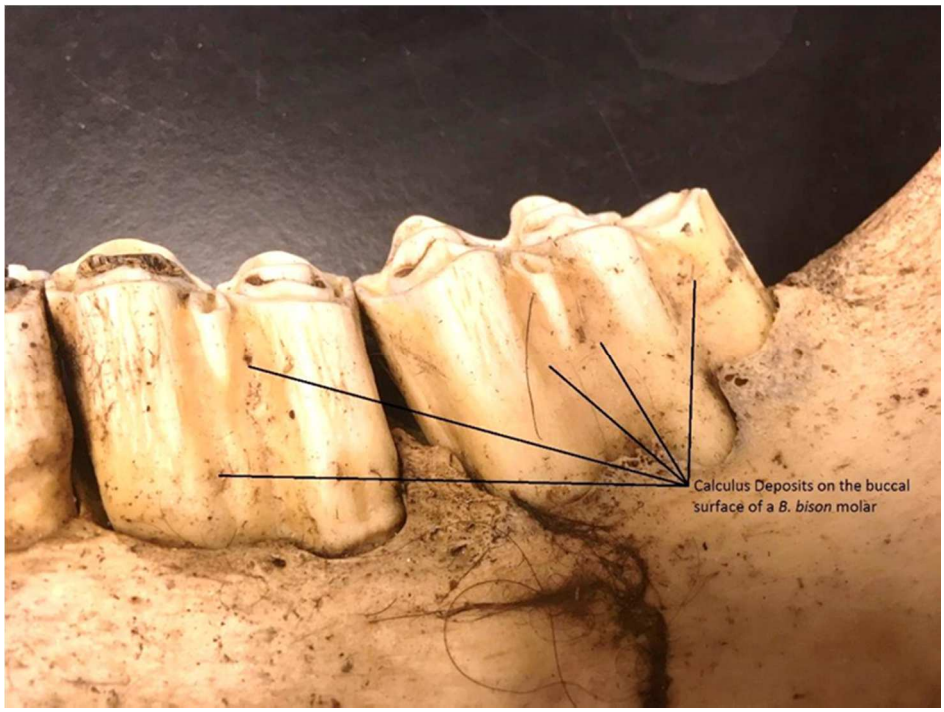

Figure 1: Photo showing common calculus deposit locations on a modern bison mandible. Calculus appears as a white to beige/yellow deposits on the surface of the tooth.

Dental calculus phytoliths has been used on mastodons, mammoths, modern elephants as well as bison, domestic cattle, sheep and horses (Armitage 1975; Gobetz and Bozarth 2001; Cordova and Agenbroad 2009; Cordova and Avery 2017). This method of phytolith analysis runs into some preservation biases. Not every individual of a population is preserved, not every individual that is preserved includes preserved teeth, and not every preserved tooth has

diagnosable phytoliths embedded. Thus, this research treats all dental samples from the same site and time as cohorts, combining all of them into one observation (Cordova and Agenbroad 2009; Gobetz and Bozarth 2001; Pokines et al. 2019).

Research rationale:

The hypothesis of diminution caused by shifting grassland composition due to climate change, has more support within the literature. In this hypothesis, the literature claims that the changing climate, via the changing grassland composition, went from being dominated by nutritious C_3 grasses to being dominated by less nutritious C_4 grasses (Lewis, et al. 2010). Hill, Hill and Widga (2008), Lewis et al. (2018) and Lyman's (2004) articles examined the fossil record and addressed the issue of presence/absence of bison, as well as the temporality of their diminution. However, the claimed causes are based on qualitative observations of mortality profiles (Hill, Hill and Widga 2008) and temporal correlation (Lewis et al. 2010), rather than measurements. Bison are very adaptable mammals that thrive under many different climatic conditions (Gates et al. 2010), which may undermine the established hypotheses on diminution.

The Great Plains is a grassland-dominated ecosystem and bison are obligate grazers (Boyd 2003; Woodburn et al. 2016). This means that grass phytoliths should be common in both soil and animal samples. Therefore, the Great Plains are an ideal place to apply dental calculus phytolith analysis to add to studies of bison diets and bison ecology, by providing a direct link between the bison and the grass. If the diets observed stayed static across the study period, this could contradict that changing grassland composition was driving diminution.

There is evidence that diet did change over space and time due to bison molar wear pattern variations (Rivers, Solounias and Mihlbacher 2007), but direct data of exactly what the bison were eating at a specific locale would be beneficial. Comparing archaeological populations to modern populations may also be able to shine more light on this issue by way of highlighting the differences in diet, habitat and behavior between the temporally distinct populations.

The contribution of this research is to provide a viable supplementary methodology to fill the existing gaps in the study of bison diminution in the Great Plains. Furthermore, this research provides a link between the grass and the bison through an examination of diet, thus adding phytoliths to the broader study on bison evolution.

Research presentation

The rest of this thesis is written in a non-traditional manner. The thesis is written as an article, which will be ready to submit to journals for evaluation. This means that there will be a title and an abstract; followed by the body of this research. This document will be completed in a manner which will be easy to publish. This will be done for several reasons. The first of these is one of practicality. It is more economical to write this thesis as an article for publication now, than to write a more traditional thesis which would need to be edited down into a publishable format. Secondly the aim of this study is to effectively disseminate knowledge about a methodology, the most parsimonious way of going about this is to write the thesis in such a manner that it can be ready for publication quickly. The way we chose to write this document

is the most in-keeping with that philosophy of spreading these ideas as quickly and efficiently as possible.

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II. RESEARCH ARTICLE

Phytolith analysis as a paleoecological proxy when examining bison anatomical and behavioral changes in the Great Plains

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Abstract:

The demise of mammoths, during the terminal Pleistocene extinction event, thrust bison into a role as both the keystone herbivore of the Great Plains grasslands and the most important prey resource for the established human populations. Since the end of the Pleistocene, the genus *Bison* underwent significant anatomical and behavioral changes. This study examines opal phytoliths embedded in dental calculus of prehistoric bison specimens as a proxy for reconstructing environmental context of anatomical and behavioral changes underwent by the Great Plains bison since the terminal Pleistocene. The strategy includes comparing phytolith assemblages in dental calculus on prehistoric bison across sites and with

those of modern bison in various types of grasslands. The prehistoric bison examined were sourced from the Beaver River Bison Hunting Complex, the Ravenscroft II Bison Kill Site and the Folsom Site, in Oklahoma and New Mexico. This research shows that phytolith analysis is a viable method of adding additional data to other studies on bison paleo-ecology. The phytolith counts obtained indicate a significant climatic and potential ecological difference between the ancient bison and the modern references which were analyzed.

Introduction:

The extinction event occurred in North America c. 13,000 BP removed, along with many other species, the Columbian mammoth (*Mammuthus columbi*), the dominant keystone herbivore of the American grasslands (Knapp et al. 1999; Graham 2001; MacDonald 2003; Bison and Carter 2014). Through its role as the keystone herbivore, the Columbian mammoth was essential to the maintenance of this ecosystem, to the point that many other species depended on the mammoth's existence (Graham 2001; Barnosky et al. 2016; Malhi et al. 2016). This included other herbivores that benefitted from the ecosystem management performed by the mammoths as well as carnivore species to whom mammoths were an important source of protein.

After the demise of the Columbian Mammoth, bison evolved to fill this newly vacated role of principal plains herbivore and the role of primary prey species to several predators, including the human population, who had previously been dependent on mammoths for their protein intake (Wyckoff and Dalquest 1997). In their new role, bison helped change and shape

the plains environment into the recognizable historical landscape that Europeans encountered just a few hundred years ago (Knapp 1999; Boyd 2003). During this period, the bison itself evolved, the ecosystem changed the bison as the bison changed the ecosystem (Wyckoff and Dalquest 1997). Some of the changes bison underwent in this period are evident in the fossil record, which show that bison became smaller over time, a process called diminution in the literature, and began to amass in much larger herds. However, the underlying mechanism for this evolution of morphology and behavior is yet not fully understood. *Bison* went locally extinct in some areas before cropping back up, all the while evolving to be better adapted to the ecosystem. Evolution is driven by ecological change and the changes that occurred in the Great Plains still hold some mysteries (Rivers, Solounias and Mihlbacher 2007; Lyman 2004)

The available materials from many prehistoric sites have provided proxy data for reconstructing the environments where bison lived (Calson et al 2018; Carlson 2015; Bement et al. 2012; Johnson and Bement 2009), providing ample evidence of the substantial changes bison and their ecosystems in the North American Great Plains underwent. In particular, $\delta^{13}C$ and other stable isotope analyses have provided information on dietary and environmental changes (Carlson et al 2018; Widga, Walker and Stockli 2010; Johnson, Willey and Macpherson 2007; Feranec 2007; Hoppe, Payton and Chamberlain 2006).

Isotopic fractionation of organic carbon and nitrogen constitutes a useful paleoecological datum, including age, percent C_4/C_3 photosynthetic pathway in herbivore remains, carnivore diet through secondary isotopic fractionation, as well as migratory and dispersal patterns (Den-David and Flaherty 2012). However, there are weaknesses in that

methodology as it is impossible to distinguish between one C_4 plant and another, even within remains of obligate grazers. Where more precision is needed, this method should be supplemented with an alternative. This is especially true in cases where the research question relies on the composition of the floral assemblage in a location (Widga, Walker and Stockli 2010).

However, the capability of phytolith analysis to provide insight into floral composition represents an important contribution to the reconstruction of prehistoric bison and their ecosystems. Through phytolith analysis, it is possible to identify not only grasses from other plants, but also various taxonomic groups of grasses, which are indicative of certain environmental conditions (Piperno 2006; Stromberg et al. 2018).

The dental calculus phytolith approach has been used on many herbivores, from the exotic, mastodons, mammoths, modern elephants to the more mundane like domestic cattle, sheep and horses (Armitage 1975; Gobetz and Bozarth 2001; Cordova and Agenbroad 2009; Cordova and Avery 2017). Phytoliths become embedded in the tooth calculus, colloquially known as plaque, of herbivores (Pokines et al. 2019; Middleton and Rovner 1994; Gobetz and Bozarth 2001; Cordova and Avery 2017; Bozarth and Hofman 1998; Armitage 1975). When herbivores feed, they consume plants that contain phytoliths and there is a chance that some of these phytoliths become trapped in the calculus buildup on the teeth. This calculus can then be extracted and processed so that the phytoliths can be examined, diagnosed and counted. The researchers in the literature then use these counts to determine the diet of the individual

herbivore (Pokines et al. 2019; Middleton and Rovner 1994; Gobetz and Bozarth 2001; Cordova and Avery 2017; Bozarth and Hofman 1998).

The results provided by dental calculus phytoliths assist in reconstructing several behavioral patterns of herbivores in relation to their roaming environment. One aspect is the dietary reconstruction as remains of phytolith in dental calculus indicate the plants animals have been grazing or browsing on (Gobetz and Bozarth 2001). They are also used to indicate possible migration patterns if the distribution of plants across biomes and vegetation types are known (Cordova and Avery 2017). The migration patterns approach can be applied to kill sites where dental calculus phytoliths from groups of individuals may indicate movement patterns. Thus, the study presented here uses the dietary and migration pattern approaches for reconstructing bison behavioral patterns using dental calculus from bison at different Paleoindian kill sites in the southern Great Plains (Fig. 1).

Additionally, to help test the usefulness of phytoliths in reconstructing dietary and migration patterns in prehistoric bison, this study compares the phytolith assemblages from bison from archaeological kill sites to modern bison dental samples as well as assemblages from modern soil samples of various types of grasslands (Fig. 1). These results will be analyzed in the context of what can be learned from them to illuminate the greater picture of bison evolution, within the framework of evaluating the methodology for further use within this academic niche.

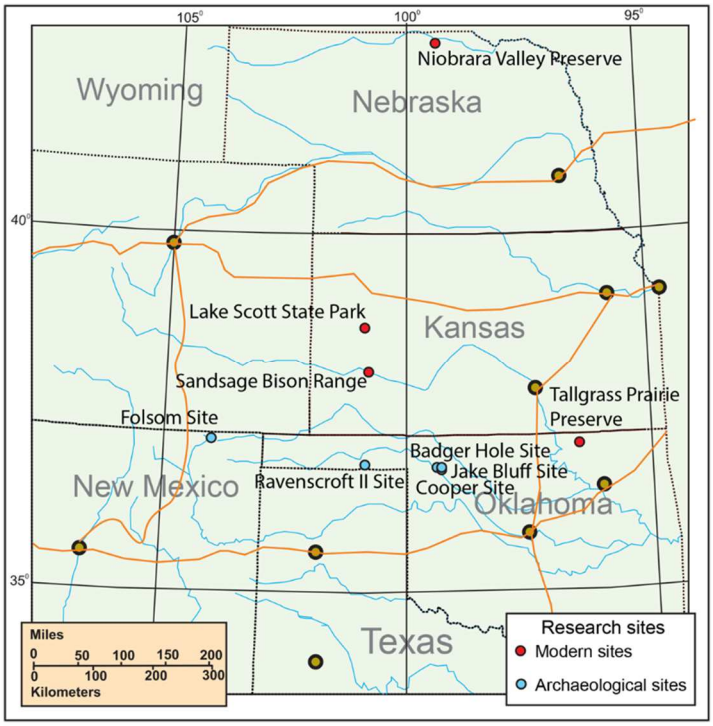

Figure 1. Locations of all study sites. Locations are color coded in order to differentiate between modern and archaeological locations. Map ranges from the edge of Minnesota in the northeast, Arkansas in the southwest, New Mexico in the southwest and Wyoming in the northwest

Study areas and localities:

Modern study areas:

The modern sites of this study include the Niobrara Valley Preserve, the Sandsage Bison Range, the Tallgrass Prairie Preserve and Lake Scott State Park (Fig. 1). Dental calculus samples and surface soil samples were obtained from the Niobrara Valley Preserve, the Sandsage Bison Range and Tallgrass Prairie. Lake Scott State Park does not have bison; thus, only soil samples were collected to provide an example of the typical shortgrass prairie of the High Plains.

The Niobrara Valley Preserve, managed by The Nature Conservancy, occupies an area of 219 km2 along Niobrara River and parts of the Sand Hills in Brown, Cherry and Keya Paha counties in Nebraska (Fig. 1). It contains an interesting mix of floral communities including influences from both the eastern deciduous forest and the western rocky mountain ponderosa pine communities (Churchill, Feeman and Kantak 1988). Three different grassland communities that occur in the preserve; these are the tallgrass prairie, the Nebraska Sand Hills prairie and the mixed prairie (Churchill Feeman and Kantak 1988). The distributions these grasslands are confined by soil characteristics generally predicated on proximity to the river, with tallgrass occurring in the floodplains, the sand hills on the stabilized dunes near the river, and mixed prairie occurring on the higher tablelands (Churchill Feeman and Kantak 1988). The average yearly temperature for the nearest weather station in Valentine, Nebraska, is 9 °Celsius (National Environmental Satellite, Data, and Information Service 2018). The annual precipitation for 2018 was 88 centimeters (National Environmental Satellite, Data, and Information Service 2018).

The Tallgrass Prairie Preserve, located in Osage county, Oklahoma (see figure 1), is also managed by the Nature Conservancy. It has an area of 154 km^2 and a variety of habitats, of which 90% is grassland (Palmer 2007). The grasslands consist of mostly tallgrass prairie with some shortgrass in areas of high grazing and areas of shallow soil (Palmer 2007). The average yearly temperature for the nearest station at Ponca City for 2018, in Ponca City, Oklahoma, is 15 °Celsius (National Environmental Satellite, Data, and Information Service 2018). The annual

precipitation is 89 centimeters (National Environmental Satellite, Data, and Information Service 2018).

The Sandsage Bison Range is located just south Garden City, Kansas (Fig. 1). Although it is located in the broader region of shortgrass prairie, this locality has sand sagebrush prairie whose grass makeup is closer to the mixed grass prairie found in areas further north and west (Rodgers 2016). The Sandsage Bison Range is only 15.22 km^2 (Rodgers 2016). The average annual temperature is 12 °Celsius, with the mean annual precipitation of 64 centimeters (National Environmental Satellite, Data, and Information Service 2018), measured in adjacent Garden City, Kansas.

Lake Scott State Park is located in Scott County, roughly 55 miles north of Garden City and 60 miles east of the Colorado border (Fig. 1). The floral species diversity found here is high for western Kansas, due to the adjacency of Lake Scott to more xeric environments, this has the effect of it being a mostly shortgrass dominated area with some aquatics and mixed grass areas also appearing, especially close to the water (Stramel 1992). The average annual temperature is 11 °Celsius with a mean annual precipitation of 56 centimeters (National Environmental Satellite, Data, and Information Service 2018) recorded at nearby Goodland, Kansas.

Prehistoric bison sites:

The prehistoric dental samples were obtained from five archaeological sites. These are the Folsom site in New Mexico, the Cooper, Badger Hole and Jake Bluff sites from the Beaver

River Bison Hunting Complex in western Oklahoma, and the Ravenscroft II site from the Oklahoma panhandle (Fig. 1). All samples within this group were provided by the Oklahoma Archeological Survey, unless otherwise noted.

The oldest of the archaeological samples originate from the Jake Bluff site. The Jake Bluff site is located between Badger Hole and Cooper in the Beaver River Bison Hunting Complex (Bement et al 2012) (Fig. 1). This site is an arroyo kill site of *Bison antiquus* which is generally typical of the Folsom culture but this locality does not fall within the accepted date range for Folsom sites (Bement et al 2012). The Jake Bluff site is late Clovis in age and contains lithics typical of the Clovis cultural complex (Bement and Carter 2010, Bement et al 2012). The remains of the 22 individuals killed here are all of the *Bison antiquus* species and were killed during September or October (Bement and Carter 2010). This site's median date is 12,712 ± 122 cal yr BP (Bement and Carter 2010, Carlson et al 2018), which makes it about a hundred years before the beginning of the accepted dates for the Folsom culture. In fact, the bonebed at this site is overlain by Folsom age lithics, separated by a meter of sandy loam (Bement and Carter 2010).

The Cooper Site lies just north of the Beaver River in western Oklahoma, near Fort Supply (Bement 1999, Johnson and Bement 2009) (Fig. 1) and is the second oldest in the sample. It has extra significance due to it being the origin location of the oldest painted object in North America, which is a *Bison antiquus* skull with a red ochre lightning bolt painted on the frontal bone (Bement 1999). This site is also of the arroyo type, part of a group of sites along the Beaver River, which are known as the Beaver River Bison Hunting Complex (Bement 1999,

Johnson and Bement 2009). This site is also associated with the Folsom cultural complex (Bement 1999, Johnson and Bement 2009). The site includes three distinct bone beds; the samples for this study included bison specimens from the middle Cooper bone bed which has a median date of 12,569 ± 47 cal yr BP (Johnson and Bement 2009; Carlson 2015; Surovell et al 2016; Carlson et al 2018). The lowest bone bed contains a minimum of 20 individuals, whereas the middle and upper kills both have a minimum of 29 distinct individuals, although the kills may be much larger as the site is quite eroded (Bement 1999; Johnson and Bement 2009).

Of the ancient sites under consideration for this investigation the Folsom site is arguably the most culturally significant, as it is the type site for the Folsom Cultural complex (Meltzer 2006). Located in Wild Horse Arroyo, near Folsom, New Mexico (Fig. 1), the site has been dated to a median date of 12,450 ± 86 cal yr BP (Meltzer 2006; Surovell et al 2016). This places it within the Younger Dryas climatic event (Meltzer and Holliday 2010; Surovell et al 2016). This site has bison remains of the *Bison antiquus* species (Meltzer Todd and Holliday 2002; Meltzer 2006). The site contains an estimated 32 individual bison which were killed during the late fall in the arroyo kill style typical of Folsom kill sites, where hunters would drive the bison into the blind arroyo and then hunters stationed on the tops of the steep banks would dispatch the trapped animals. The slain bison would then be butchered in situ, rather than removed to a camp for processing (Meltzer Todd and Holliday 2002; Meltzer 2006). The samples from this site were obtained from the Denver Museum of Nature and Science from teeth collected during the Figgins expedition.

The Badger Hole site, also belonging to the Beaver River Bison Hunting Complex, is located on the north side of the Beaver River in western Oklahoma, several hundred meters to the west of the Cooper site (Bement et al 2012) (Fig. 1). The bison here were killed in the late summer or early fall and the site contains remains of a large kill (20+ individuals) in the arroyo style typical of the Folsom cultural complex (Bement et al 2012). This site dates to 12,145 ± 79 cal yr BP (Bement et al 2012, Carlson et al 2018), and contains remains of the Bison antiquus species (Bement et al 2012).

The Ravenscroft II site is the youngest of these archaeological sites included in this study and is located in southwestern Beaver County, in the Panhandle region of Oklahoma, just north of the Texas border (Fig. 1). The site, located at the bottom of an arroyo, is a large kill site, potentially consisting of 100 or more bison killed during the winter, which possibly indicates a change in herding behavior occurring within this intermediate species (Muhammad 2017). The site dates to the Paleo-Indian period after the accepted end of the Folsom Cultural Complex (roughly 12,078 ± 72 cal yr BP) (Carlson et al 2018; Muhammad 2017). This site dates to 10,545 cal yr BP (Carlson et al 2018; Muhammad 2017) which postdates the end of the Younger Dryas Climatic Event, which was at roughly 11,650 years ago (Meltzer and Holliday 2010; Surovell et al 2016; Carlson et al 2018). The bison here are of the species *Bison occidentalis,* which is an intermediate form between the larger, heavier *B. antiquus* and the smaller, more gracile *B. bison* (Muhammad 2017).

Methods:

Sampling:

To prepare each dental sample for processing, each sample tooth was washed using distilled water and cleaned with a soft bristled brush to remove any remaining soil. This is required because we want to avoid phytoliths contained in the adhered soil to contaminate the calculus sample. The cleaned teeth were then allowed to dry overnight. Once the samples were dry, the calculus was scraped off the tooth using dental equipment. Scraping each type of bison tooth presents their own challenges. On incisors, any calculus is generally located on the palatal surface of the tooth, around the original gum line. Calculus appears as a beige to yellow deposit on the enamel of the tooth. On teeth that were subjected to intense weathering before burial, distinguishing between calculus and enamel can be challenging, however enamel will not effervesce under application of dilute HCl, which is a reliable way to determine a positive identity of a sample. The more rugose molars have folds of enamel where larger amounts of calculus accumulate. It is crucial not to scrape off the calculus too hard, as it may dislodge diminutive amounts of enamel from the surface of the tooth. Fragments of enamel will not dissolve in HCl and may occlude phytoliths during the final microscope analysis.

Sample processing and phytolith extraction:

To process these samples there are several different protocols in the literature (Armitage 1975; Gobetz and Bozarth 2001; Piperno 2006; Cordova and Avery 2017; Stromberg 2018; Pokines et al 2019) as each investigator uses a slightly different method. However, the

protocol used in this research is an adaptation to Cordova and Avery's (2017) methodology, which is simple and cost effective.

Once the calculus has been scraped off the tooth, further pressure with the dental tool was applied to break up the calculus isolate into a powder, if not already in a powdery state, this is done to ease the digestion process (Cordova and Avery 2017). The powdered sample is then weighed.

Dental calculus is formed from calcium carbonate ($CaCO_3$), so we added a solution of 35% HCl, which reacts with the calcium and forms bubbles. The reaction is concluded, and digestion is complete, when the sample stops bubbling. To remove the acidity, the sample is diluted with distilled water, centrifuged and decanted (Cordova and Avery 2017; Pokines et al 2019). We perform this step a minimum of seven times, which reduces the acidity of the sample solution to neutral. Any non-carbonate material that was trapped within the tartar will remain, this includes the phytoliths mixed with unwanted detritus. The remaining material is then suspended using distilled water and a vortex genie. This suspended sample is then pipetted onto a cover slip and allowed to fully dry. This coverslip is placed onto a microscope slide prepared with an Entellan mounting medium which is allowed to harden over several days. This allows for a more permanent slide and the heavy mounting medium floats all the phytoliths onto a single viewing plane (Cordova and Avery 2017) which aids in observation and identification.

Microscope identification and counting:

Once the slide is prepared the number of phytoliths are counted. To accomplish this, each slide was observed using a light refraction microscope at 400x magnification. The slide is viewed in a grid pattern to ensure that we scan the entirety of the sample and obtain an accurate count. Any observed phytoliths are identified and recorded. Under a microscope phytoliths appear as silvery and opalescent. Unfortunately, the dental calculus numbers for phytoliths are highly variable, especially from the archaeological sites, so each scraping from a sample was observed separately and then summed to form a single statistical cohort for each site location. The cohort grouping approach allows for larger phytolith totals per sample locality.

The extraction methods described above do not require highly corrosive chemicals that may erode or dissolve phytoliths (Cordova and Avery 2017). The tradeoff is that this methodology makes phytoliths slightly more difficult to see under the microscope as there will still be some other unwanted materials present in the sample, such as organics, tooth enamel fragments and sediment particles. However, with prehistoric samples like this it is imperative to preserve as much of the raw data as possible due to the inherent variability of the observed counts (Cordova and Avery 2017).

Plotting and analytical tools:

Once counts are obtained for both the modern and ancient site samples, a limited statistical analysis was performed. The graphs generated were created using C2 program, version 1.1.7 (Juggins 2014). The distribution of phytolith morphotypes discussed included only

grass morphotypes, as they are the most abundant in the soil and dental calculus samples, and the only ones relevant to this study. The distinction of morphotypes includes the typical short cells, elongates, trichomes, and bulliforms (Fig. 2). The diagnostic short cells, which are the ones useful for determining grass subfamilies, are the commonly used grass silica short cells (GSSC) (Stromberg et al. 2018; Cordova and Avery 2017 Barboni Bonnefille Alexandre and Meunier 1999) (Fig. 2)

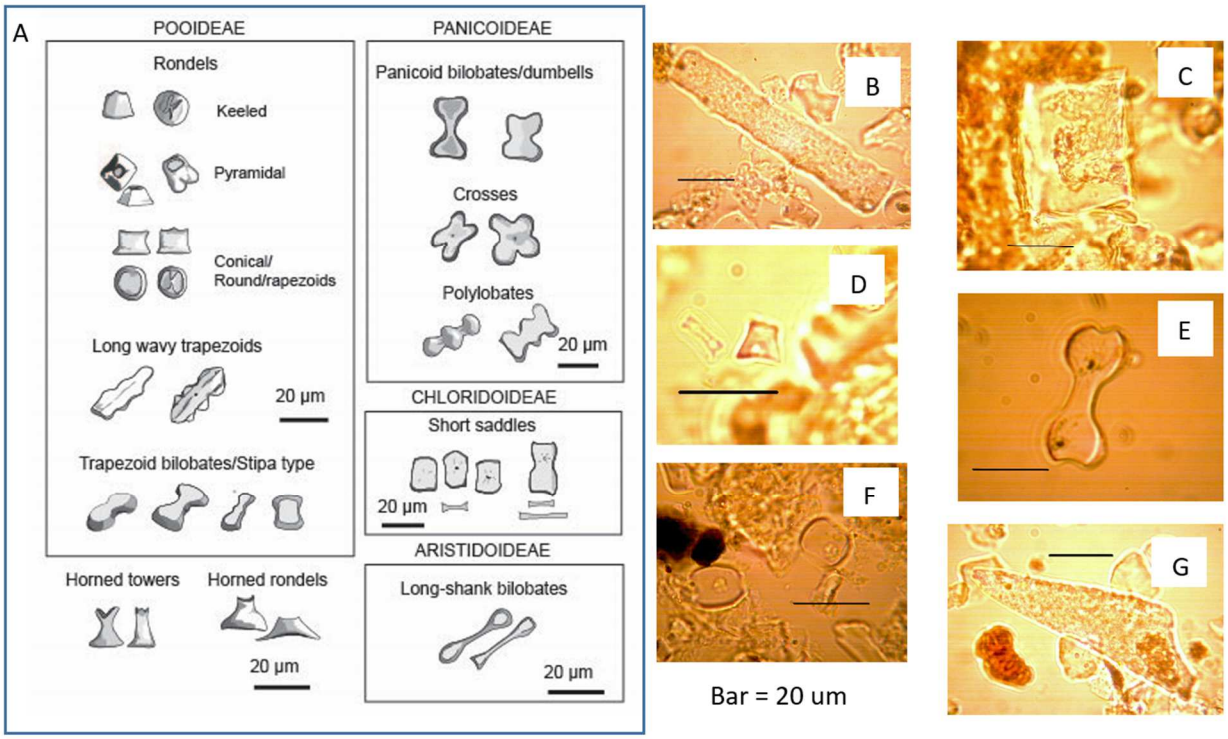

Figure 2. Phytoliths. Chart shows diagnostic phytoliths with their associated families. A. GSSC. B. Elongate, non-diagnostic. C. Rectangular bulliform, non-diagnostic. D. Typical rondel, diagnostic Pooideae. E. Panicoid bilobate, diagnostic panicoideae. F. Short saddles (2), diagnostic Chloridoideae. G. Trichome, non-diagnostic

Multivariate statistical analyses included cluster analysis and principal component analysis (PCA), performed using Paleontological Statistics (PAST) software (Hammer, Harper and Ryan 2001). Cluster analysis using Bray-Curtis ordination permitted measuring the similarity of the samples as normal statistical tests cannot be run on this data due to the one observation per site nature of this data (Beals 1984, Rogerson 2015). PCA permits a visual comparison between the phytolith assemblages (Fredlund and Tieszen 1994). These two multivariate techniques helped comparing the nature of the prehistoric and modern phytolith assemblages with those of modern soils from selected modern grassland ecosystems.

Results:

In total 47 samples were analyzed, 11 were from soil samples and 36 from dental calculus. The numbers obtained from the soil samples were invariably high, counting was stopped on a slide once a count of 200+ total phytoliths had been observed. The dental samples were far more variable, although modern samples generally included more identifiable phytoliths than the ancient samples. Although many broken or deteriorated phytoliths existed in some samples, in this study only identifiable phytoliths were included. In this case, identifiable means the phtoliths whose original morphotypes could be determined (i.e., those in Fig. 2).

The ancient dental calculus samples displayed high variability of numbers among the samples, with the sample from the Folsom site containing only five identifiable phytoliths and one from the Cooper site including 81 identifiable phytoliths. The modern dental calculus

samples displayed even more variability, although a much higher average phytolith count. The minimum count was four, from a highly weathered dental sample from the Tallgrass Prairie Reserve and the maximum was 229 from a mandible from the Niobrara Valley Preserve.

The distribution of observed phytolith morphotypes from the soil and dental calculus samples appear distributed by number and percentage in the tables and graphs in the Appendix, where the counts and percentages of the soil samples appear already combined by locality. Likewise, the counts of the modern and ancient dental calculus samples appear grouped by locality.

Total Observed Phytoliths:

Once summed, the phytolith totals were as follows. The Niobrara Valley Preserve soil sample group had 616 total observed phytoliths, 559 total GSSC (grass silica short-cell), of which 405 were diagnostic (Fig. 2, C). The Tallgrass Prairie Preserve soil sample group had 621 total observed phytoliths, with 536 GSSC, of which 422 were diagnostic, from 7 samples. The Sandsage Bison Range soils sample group had 609 total observed phytoliths, with 474 GSSC, of which 380 were of the diagnostic The Lake Scott State Park soil samples contained 417 total observed phytoliths, with 343 GSSC, of which 305 were diagnostic.

Of the modern dental samples, the Niobrara Valley Preserve dental sample contained 867 total observed phytoliths, with 814 GSSC, of which 638 were diagnostic, from 4 samples. The Tallgrass Prairie Preserve dental sample contained 876 total observed phytoliths, with 726

GSSC, of which 517 were of diagnostic, from 7 samples. The Sandsage Bison Range dental sample group contained 335 total observed phytoliths, with 258 GSSC, of which 166 were diagnostic, from 2 samples.

In the samples obtained from the archaeological sites, the total numbers of observed phytoliths were smaller. In the dental sample obtained from the Folsom site, a total of 94 phytoliths were observed, with 59 GSSC, of which 41 were diagnostic, from 5 samples taken from 5 individuals. From the Cooper site samples, 287 total phytoliths were observed from seven different prepared slides, of these 203 were GSSC, of which 144 were diagnostic. These slides were prepared from 7 teeth taken from the slump of the bluff, which came from an unknown number of individuals. From the Ravenscroft II samples, 89 total phytoliths were observed, with 54 GSSC, of which 43 were diagnostic. These five samples were obtained from 5 teeth of unknown individual provenance. From the Badger Hole site samples, 68 phytoliths were observed, with 46 GSSC, of which 31 were diagnostic. These 2 samples came from a single fracture mandible representing one individual. From the Jake Bluff samples, 56 total phytoliths were observed, with 29 GSSC, of which 22 were diagnostic. These four samples originate from two individuals.

Once count totals had been obtained, each sites' totals were transformed into percentage counts so that direct comparisons between samples could be done (Rogerson 2015). Thus, Figure 3 shows the distribution of GSSC, and Figure 4 shows the distribution of elongates, trichomes and bulliforms; as well as the GSSC percentages grouped by family, and the GSSC-derived indices.

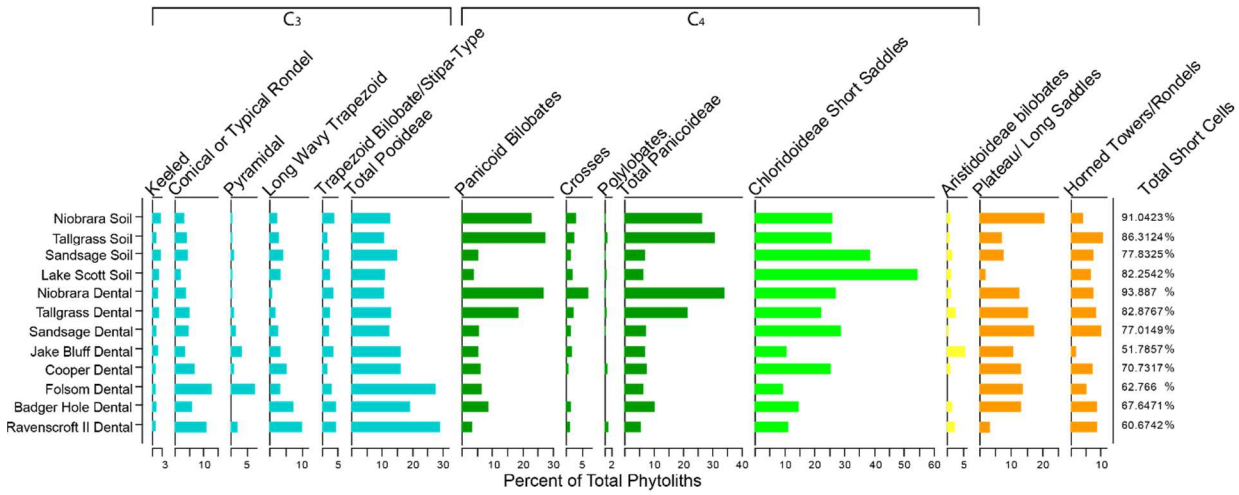

Figure 3. Graph showing percent total phytoliths across GSSC morphotypes. Pooideae are in blue, Panicoideae are in dark green, Chloridoideae are in bright green and Aristodoideae are in yellow. Non-diagnostic short cells are in orange.

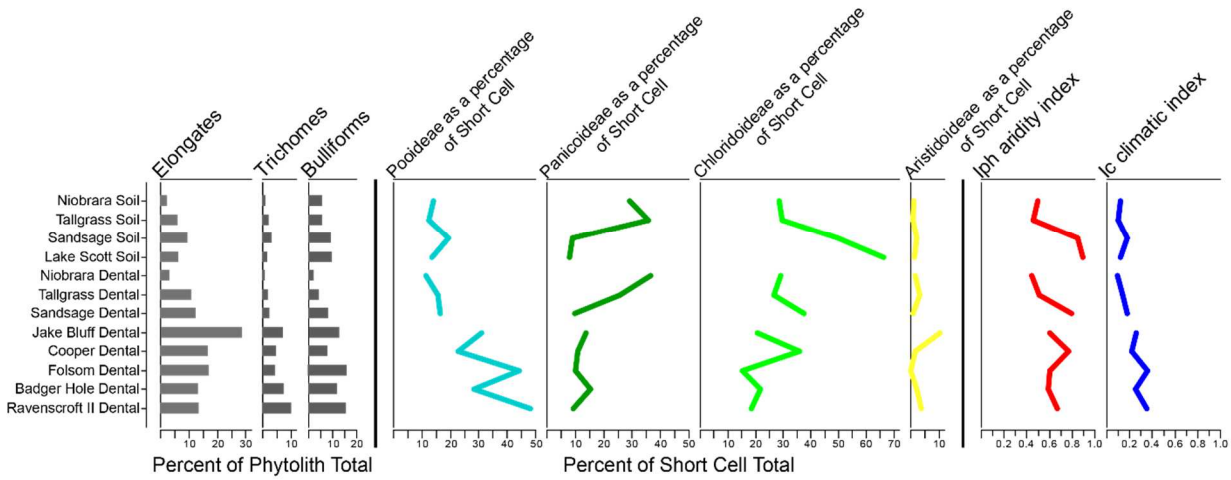

Fig. 4. Percentages of elongates, trichomes and bulliforms; GSSC percentages by subfamilies, and GSSC-derived indices. Breaks separate data types.

Modern phytoliths by grass subfamily:

The phytolith values obtained from the samples match the characteristics known about each location relatively well (Piperno 2006, Stromberg et al 2018, National Environmental Satellite, Data, and Information Service 2018). The values obtained for the Pooideae, C_3, grasses remain relatively constant over each of the modern site locations, from a minimum of 12.5% of the GSSC total, at the Tallgrass Prairie Preserve, to a maximum value of 19.2% obtained from the Sandsage Bison Range. Among the ancient sites, these values were higher, with a maximum observed rate of 48.1% of the GSSC phytoliths observed within the Ravenscroft II sample (Fig. 3). The Panicoideae, C_4, grasses had their maximum value observed at the Tallgrass Prairie Preserve, at 35.6% of the GSSC sample and a minimum of 7.8% at Lake Scott State Park in the more arid environment found there. Within the other half of the samples, the values ranged between 9.3% of the diagnostic sample observed from the Ravenscroft II site and 15.2% from the Badger Hole site (Fig. 3). Chloridoideae grasses were far more numerous in the more xeric modern environments, with the maximum value obtained from the typical shortgrass prairie found at Lake Scott, which totaled 66.2% of the GSSC sample, and the minimum value observed was 28.4%, which was obtained from the Niobrara Valley Preserve. This appears to be the case within the archaeological sites as well with the largest percentage recorded at the Cooper site sample at 36.0% and the smallest being 15.3% from the Folsom site (Fig. 3). Aristidoideae had low values across the board, with values falling between 0 and 3.2% except for the Jake bluff dental sample where this family formed 10.34% of the GSSC sample, however this is expected to be due to the low sample size of total diagnostic phytoliths within the Jake Bluff sample (Fig. 3).

GSSC-derived indices:

The I_{ph} aridity index, returned values for the archaeological sites of between 0.59 for the minimum value at Badger Hole, and a maximum value of 0.77 at the Cooper site (Fig. 4). These values fit neatly between the values returned for the dental samples of two of the modern analogs, as the Tallgrass Prairie Preserve returned a value of 0.51 and the Garden City dental sample returned a value of 0.80 (Fig. 4).

The climatic index, I_c, which indicates prevailing temperatures, shows very different values for the ancient sites as compared to the modern analogs. The modern sites returned values of between 0.15 and 0.23 for the soil values (Fig. 4). The dental values were a bit more varied, falling between 0.15 and 0.25. The archaeological sites returned very different values from those previously discussed as the minimum value among this cohort was calculated from the Cooper site sample at 0.32 while the maximum value observed was 0.63, which was recorded from the Folsom sample (Fig. 4).

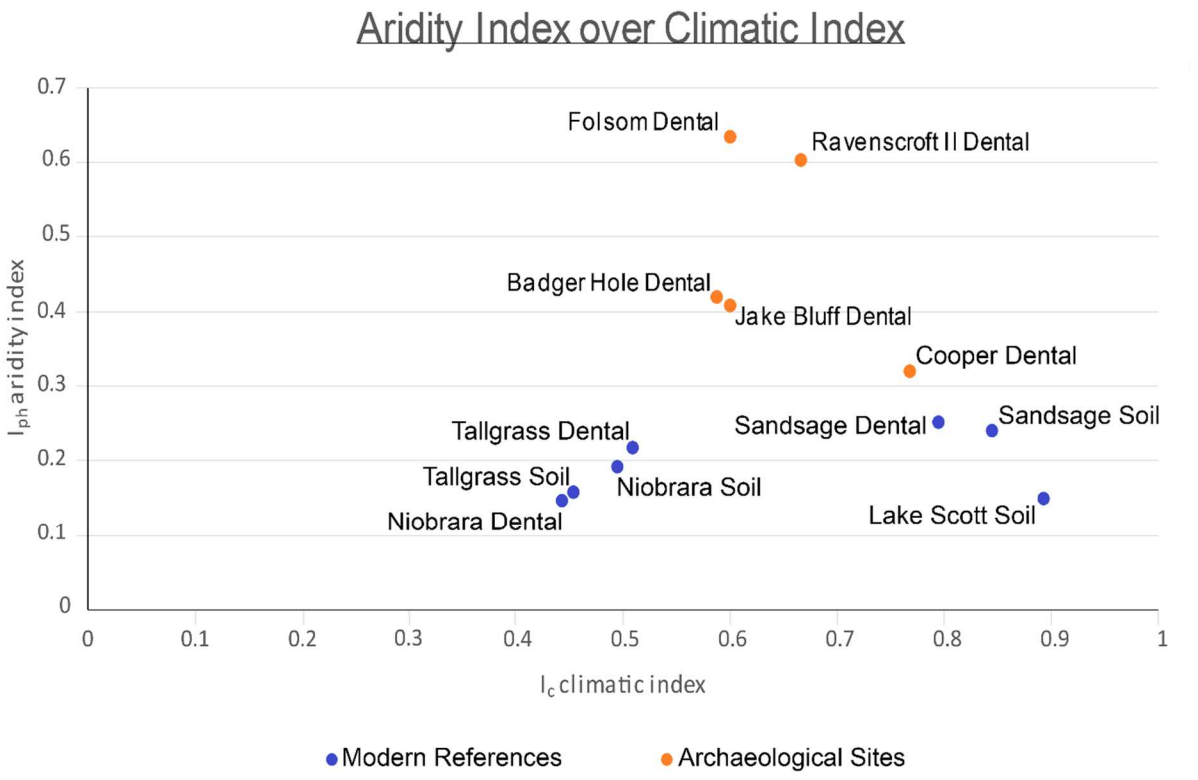

Figure 5. Scores for I_{ph} and I_c plotted against each other.

To gain a better understanding of groupings and similarities between sites the vales obtained for I_{ph} and I_c were plotted against each other (Fig. 5). Samples with similar characteristics of aridity and temperature should be located close to each other on this graph. Interestingly we see three groups forming out of these values, these are the Niobrara and Tallgrass group; the archeological sites; and Sandsage, Cooper and Lake Scott group.

Multivariate Sample Characteristics:

Once samples were obtained they were subjected to statistical analysis. Due to the nature of our data and the fact that this paper uses summed data totals by necessity, this precluded the use of most statistical tests that use sample means.

To compare similarities in the sites, a cluster analysis was performed, this was completed using a Bray-Curtis dissimilarity matrix based on the transformed values for the diagnostic phytoliths. This matrix noted two main groups. Broadly these were the modern samples in the first cluster and the archaeological samples in the second, with one notable exception. The Cooper dental sample was found to be most similar to the Garden City dental sample (Fig. 6).

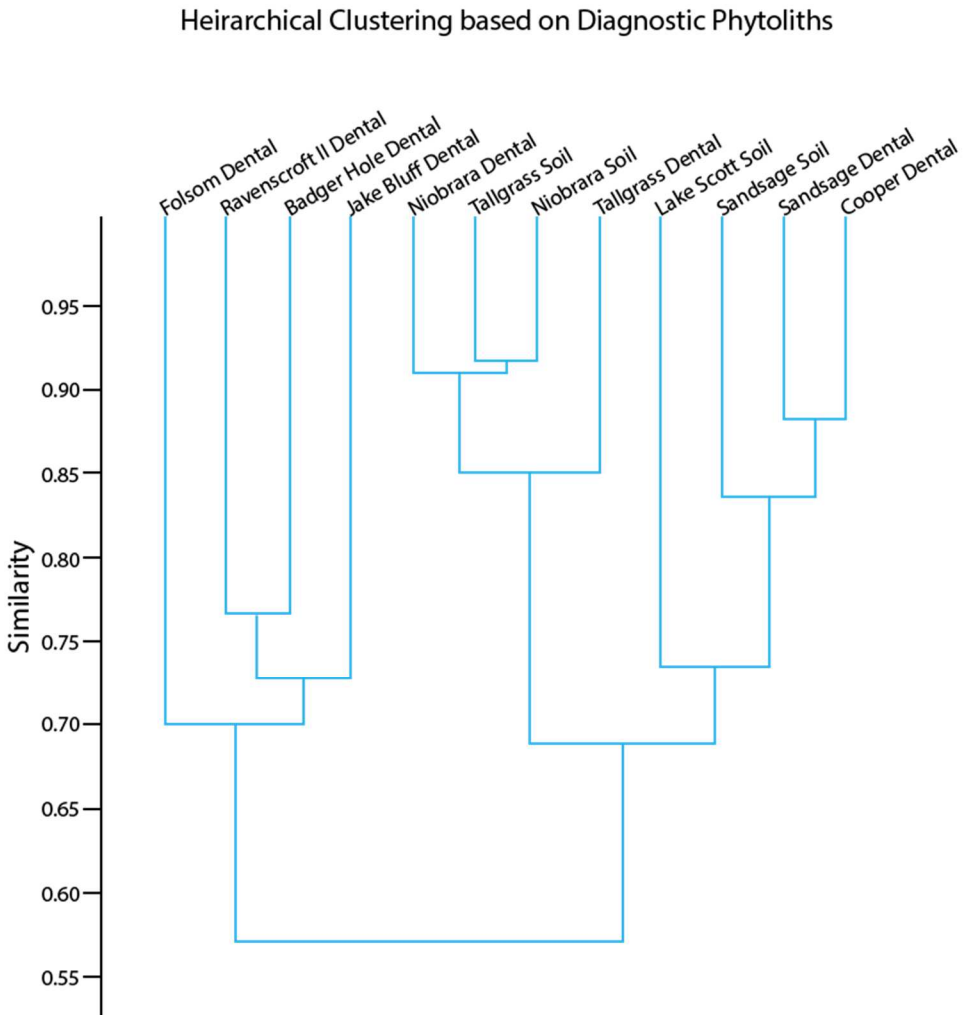

Figure 6. Cluster dendrogram showing similarity values of diagnostic GSSC at each site and using the Bray-Curtis matrix. Note the two distinct groups, Modern + Cooper and Ancient. Also, note the similarity of Cooper to the Sandsage site.

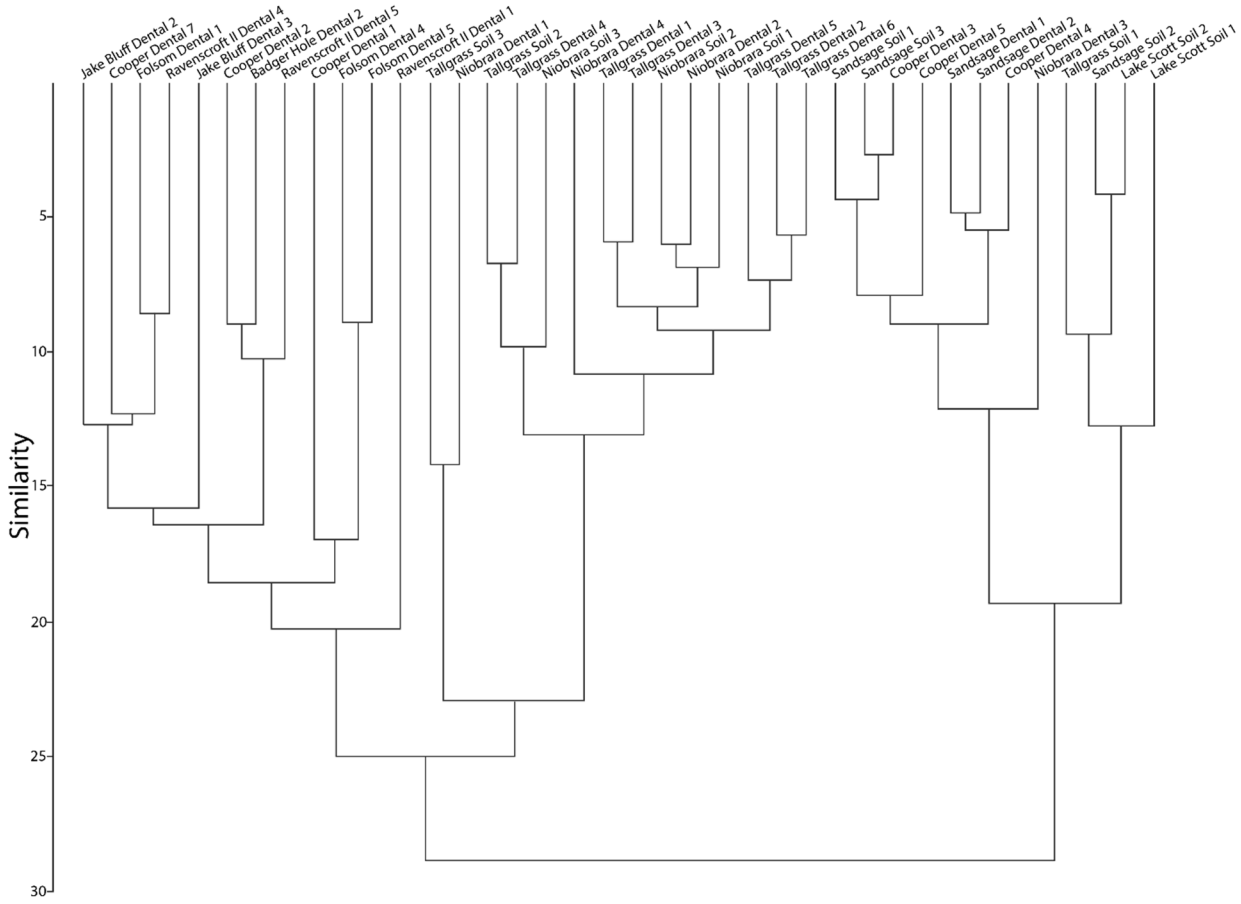

Figure 7. Clustering of individual samples with > 15 phytoliths. Note that Cooper 3, 4 and 5 group with the Lake Scott and Sandsage samples while Cooper 1, 2 and 7 group with the other archaeological samples.

To try to determine why the Cooper site sample was grouping with the modern sites, a cluster analysis was performed on the data from each individual sample slide (Fig. 7). Slides were not included if they had fewer than 15 total phytoliths. In general, the same groups are

formed; the Niobrara and Tallgrass group; the archeological sites; and Sandsage, Cooper and Lake Scott (as well as single samples from Niobrara and Tallgrass). Interestingly not all the Cooper samples are found in that third group. There are three samples from Cooper that group with the rest of the archaeological samples (Fig. 7). This indicates a certain bimodality within the Cooper site samples, which is caused by the large proportion of Chloridoideae phytoliths within half of the Cooper samples

The Principal Component Analysis (PCA) also showed this separation between the groups. Figures 8 and 9 plot the first two principal components, which together explain 94.738% of the sample variance. Component one has the highest loading variable being the short saddle phytolith type, a diagnostic morphotype for Chloridoideae grasses (Figs. 8 and 9). Component two is defined by the Panicoid bilobate morphotype as well as the other less common Panicoideae phytoliths, with negative loadings for all other variables except the keeled Pooid morphotype (Fig. 8). The Modern + Cooper group loads neutrally to highly positive on component one and is spread out on component 2 (Fig. 8). The group that consists of the ancient sites all load close to neutrally on component 2 but are all loaded negatively on component 1 (Fig. 9).

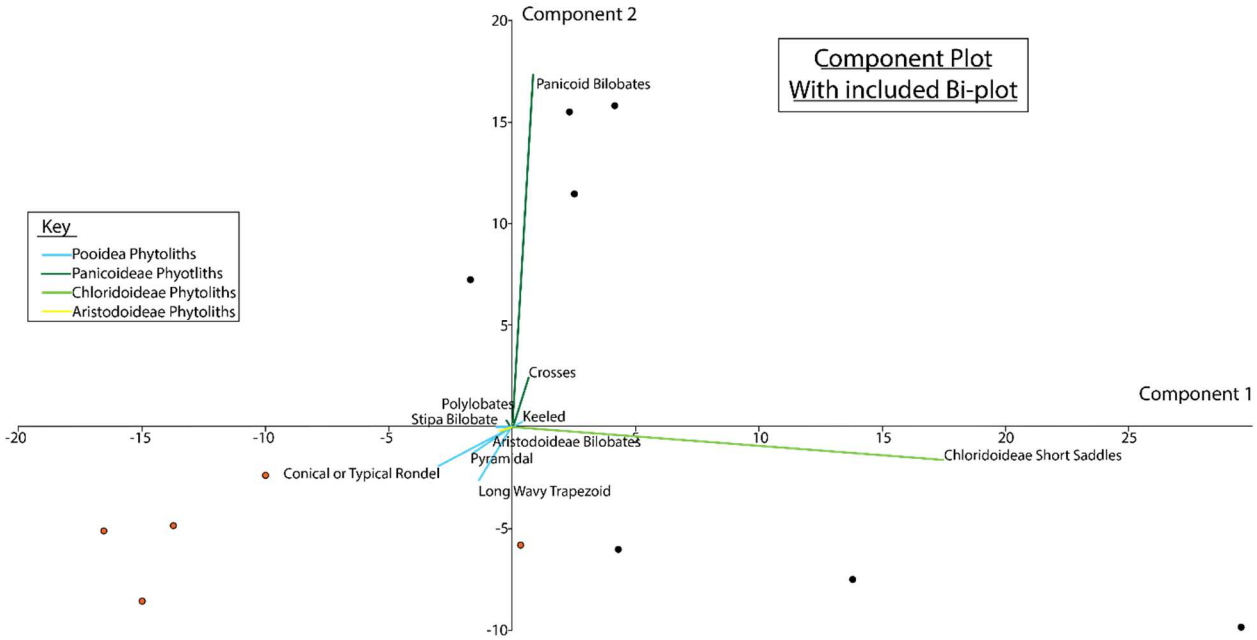

Figure 8. Principal Component Analysis Plot. Loading of diagnostic phytolith variables into the first components. Loadings are color coded by family.

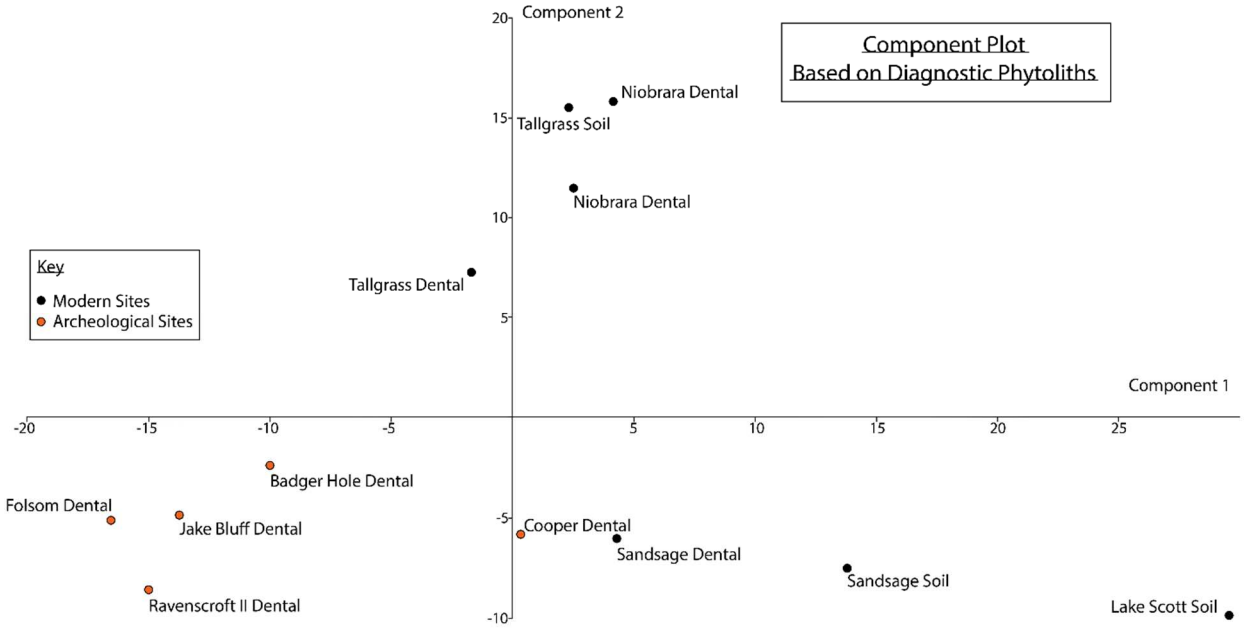

Figure 9. Principal Component Analysis Plot showing scores for each site locality. Scores are color coded by site type.

Discussion:

GSSC-based indices across ancient and modern sites:

The analysis of the two GSSC-indices calculated, show clear-cut differences among the samples. All the archaeological samples present I_{ph} values similar to the modern Tallgrass Prairie Preserve and the Sandsage Bison Range. Since Cooper showed the highest value for I_{ph} among the ancient sites this indicates that the bison killed at the Cooper site were living in the most arid environment of all ancient samples, while those at Badger Hole had the least arid environment, with an I_{ph} value of 0.59 (Nogué et al 2017). However all of these values falling between those of the two modern sites would suggest that the aridity of these sites, available water in their environment, falls somewhere between the tallgrass prairie and the mixed grassland of the Sandsage Bison Range in Garden City, KS. Which receive 78 and 64 centimeters of precipitation, respectively, per annum (Nogué et al 2017; National Environmental Satellite, Data, and Information Service 2018).

The climatic index (I_c) is a little harder to interpret as the values did not line up as well within the modern soil sites as could be hoped for. Based on studies that created and used the climatic index (Twiss 1987; Twiss 1992; Barboni Bonnefille Alexandre and Meunier 1999) the index should line up with growing season mean temperature. Thus, according to the temperature data (National Environmental Satellite, Data, and Information Service 2018), the expected I_c values in descending order would be: Niobrara, Lake Scott, Sandsage, and Tallgrass Prairie Preserve. However, the results show that this is not the case, as Sandsage has the

highest value, followed by Niobrara, Tallgrass, and then Lake Scott. Interestingly the Sandsage Bison Range and Lake Scott present very distinct I_c values, despite being only 85 km (52 miles) apart and almost at the same elevation (Fig. 1). This indicates that the Sandsage Bison range actually has the highest proportion of C_3, cool season grasses rather than the areas that actually experience colder climate. It is possible that the I_c values obtained from the other modern sites are being depressed by the high relative abundance of the other grass families found in those locations.

However, what is evident is that the values obtained from the ancient sites are very different from the ones received from the modern references. The I_c values from the modern sites range from 0.15 to 0.24 for soil samples and 0.15 through 0.25 for dental samples whereas the ancient dental samples range from 0.32 through 0.60. This would indicate that the diet of the bison sampled from these ancient sites relied far more on C_3 grasses, than their modern counterparts (Twiss 1987, Twiss 1992, Barboni Bonnefille Alexandre and Meunier 1999). This indicates either a change in dietary preference and/or that the environment they inhabited was substantially colder than the modern one.

Interestingly the lowest value obtained for I_c was from the Cooper site. This would indicate that the Cooper site was actually the warmest of the archeologic locations sampled, which conflicts with the established literature (Carlson et al. 2018) due to Cooper's position during the Younger Dryas climatic event. However, the C_3-C_4 distribution of GSSC phytoliths (Fig. 3) paralleled the data published in Carlson et al (2018) cited from Bement et al (2007). Furthermore, Bement et al (2007) also encountered a high-observed occurrence of C_4 grasses at

≈12,500 cal yr BP, the peak observed at that temporal location with lower C_4 occurrence on either side, which is temporally correlated with the Cooper site. This high proportion of C_4 grasses would tend to deflate the corresponding abundance values for the Pooid grasses and thus lower the calculated value for the I_c index (Twiss 1987, Twiss 1992, Barboni Bonnefille Alexandre and Meunier 1999). To obtain references that more closely mirror the values obtained for I_c in the archaeological sites, samples would logically have to be drawn from areas farther to the north which experience cooler growing seasons than the modern references included within this study.

The results from the multivariate perspective:

The results of the cluster analysis add evidence that Cooper is dissimilar to the rest of the ancient sites, The Cooper site bison appears associated most closely with the dental sample found in the mixed grass prairie at the Sandsage Bison Range. This strong association with a more arid environment present and Cooper could be that the climate at the time of the kill was generally warmer and more arid than the other ancient sites, which would have precluded the growth of C_3 grasses. However, independently from the general climatic conditions, the prevailing C_4 grasses may be influenced by the seasonality of the kill. Large bison kills were completed in late summer or fall, as evidenced by the seasonality of all the ancient sites included in this study, save for the younger Ravenscroft II which was a winter kill (Muhammad 2017: Bement et al. 2012; Bement and Carter 2010; Bement 1999). Kill seasonality may have been due to migration patterns which the bison followed. These bison may have lived most of

their lives in warmer climates, and transported the phytoliths to the site (Bement 2003). This hypothesis is not refuted by the published phytolith values from the Jake Bluff site, as the high values for C_4 grasses observed from the soil samples analyzed may have been due to the seasonality of the kill and contamination of the sample by the rumen contents (Bement 2009). Also the bimodality noted in the samples from Cooper in the cluster analysis of the individual samples may have played a significant part in why the measurements from Cooper are so distinct from the other sites. The age structure of the kill at Cooper was of a cow-calf herd, which could have influenced results due to the juveniles not having been weaned during the main growth of the cool season grasses (C_3) (Bement 1999), this could lead to increased proportions of the warm season grasses in the sample. Regardless, the similarities between the Cooper site and the Sandsage Bison Range are striking, the two sites rate similarly on most of the metrics evaluated.

The results for the PCA provide a similar trend in the similarities across sites. With most of the sample variance being explained by the first two factors. Component one is mostly defined positively by the proportion of Panicoid bilobates and negatively by the proportion of Pooideae phytoliths in the sample. Component 2 is mostly defined positively by the proportion of Chloridoid short saddles and negatively by the collective of Pooideae phytoliths. The clustering visually evident on Figure 6 upholds the patterns seen in the cluster analysis. All the ancient sites fill one group, then the modern plus Cooper are in another. Interestingly, the dental samples score on average 3.967 lower for component one than their associated soil value. This would indicate that the modern bison are selecting against eating Chloridoideae

grasses when other grasses are available. Unfortunately, since this study lacks soil data for the ancient sites and the published soil phytolith data for these sites appears contaminated via rumen contents (Bement 2009), it is impossible to compare this observation to the bison found at those sites. However, this preference for softer grasses is documented in the literature (Rivers, Solounias and Mihlbacher 2007), but it is impossible to endorse this hypothesis using the data obtained by this study, despite the high abundance of C_3-diagnostic GSSC in the prehistoric samples. Obtaining and including uncontaminated soil data for the archaeological sites would be a good next step to broaden the insights found during this investigation. With this data in hand it might be possible to make hypotheses about the dietary choices these ancient bison were making and those observations could further inform us about the ecology of these animals.

Conclusion:

Phytolith analysis, specifically dental calculus phytolith analysis, is proposed here as potential route toward gaining an insight into bison paleodiet and paleoecology. Despite issues with scarcity of phytoliths caused by limited sample access and lack of modern data, this study showed interesting premises useful to studies of herbivore paleodiets and paleoecology.

Firstly, it is possible to hypothesize that during most of the temporal cross-section observed through the ancient sites, it was cold. Significantly colder than it is today. The extremely high values for I_c indicate this, especially with such comparatively arid values seen in the I_{ph} values. If it had been significantly wetter, then it would be reasonable to say that the

increased moisture was driving the decrease in the climatic index values. Without that occurring, it reinforces the impression that most of the ancient sites experienced significantly cooler climate and correspondingly higher amount of cold season grass growth than any of the modern references. Further studies should include a wider array of reference sites from areas farther to the north, such as the Dakotas or Alberta.

This abundance of C_3 growth does not refute the hypotheses about bison diminution. The high proportions of C_3 grasses observed within the calculus samples of the ancient sites, with all ancient dental values > modern reference values, is consistent with the idea that the grassland composition is changing, which may be driving diminutions in the genus (Lewis, et al. 2010; Lyman 2004; Faith 2011; Hill, Hill and Widga 2008). This data cannot refute the hypothesis that human predation has played a role in bison diminutions as grassland compositional changes and human hunting pressure are not incongruent with each other, as human hunting pressures may have expedited any changes (Hill, Hill and Widga 2008).

Secondly, data from the Cooper site appeared very different from those of the other prehistoric sites. Whether that is due to a microclimate at that location, bison migration, kill age structure, or some other unrealized factor. The values seen for the Cooper site dental samples are very similar to those obtained from the modern Sandsage Bison Range in Kansas(Fig. 5) suggesting similar climatic influences and grassland composition. The Sandsage is a mixed grass prairie on top of stabilized dunes (Rodgers 2016). It is possible that Cooper was very similar. This is logical even in terms of temperature and precipitation as the values for the indexes calculated were similar as well. However, it is important to remember that even

though Cooper rated the warmest of the prehistoric sites and Sandsage had the lowest observed I_c value for any of the modern references, Cooper still rated as cooler than Sandsage. Cooper Site may also have been an outlier within its own time, locally warmer and drier than the region immediately surrounding it.

The published soil phytolith values for one of the ancient sites indicate the seasonality of the kill being in the late summer and fall, due to the high C_4 GSSC phytolith content presumably from the bison's rumens (Bement 2009). This contamination makes it impossible to use these values as indicative of the yearly mean grass growth. Therefore, further studies on dental calculus phytoliths of highly mobile herbivores should include an uncontaminated contemporaneous reference of phytoliths at the site, when possible.

Finally, the study presented here shows that dental calculus phytoliths analysis from kill sites remains a viable method for data acquisition for studies into bison diminution, particularly as supplementary data to the more utilized isotopic approach.

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III. APPENDICES

Phytolith tables including totals and percentages:

Niobrara Preserve soil samples								
Sample Number NI-	7A		1A		3		Total	
Keeled*	5	2.41	4	1.94	7	3.44	16	2.59
Conical or typical rondel*	6	2.89	8	3.88	7	3.44	21	3.40
Pyramidal*	1	0.48	0	0.00	2	0.98	3	0.48
Long wavy trapezoid*	3	1.44	7	3.39	4	1.97	14	2.27
Trapezoid bilobate/Stipa-type*	7	3.38	12	5.82	5	2.46	24	3.89
Panicoid bilobates*	48	23.18	38	18.44	55	27.09	141	22.88
Crosses*	5	2.41	11	5.33	4	1.97	20	3.24
Polylobates*	0	0.00	1	0.48	0	0.00	1	0.16
Short saddles*	57	27.53	59	28.64	43	21.18	159	25.81
Aristida-type bilobates*	2	0.96	1	0.48	3	1.47	6	0.97
Plateau/ Long saddles	49	23.67	40	19.41	38	18.71	127	20.61
Horned towers/rondels	8	3.86	6	2.91	11	5.41	25	4.05
Other non-diagnostic	0	0.00	0	0.00	2	0.98	2	0.32
Total short cells	191	92.27	187	90.77	181	89.16	559	90.74
Elongates	4	1.93	4	1.94	7	3.44	15	2.43
Trichomes	2	0.96	6	2.91	0	0.00	8	1.29
Bulliforms	10	4.83	9	4.36	15	7.38	34	5.51
Undetermined	0	0.00	0	0.00	0	0.00	0	0.00
TOTAL GRASS	207	100.00	206	100.00	203	100.00	616	100.00
Pooideae	**22**		**31**		**25**		**78**	
Panicoideae	**53**		**50**		**59**		**162**	
Chloridoideae	**57**		**59**		**43**		**159**	
Aristidoideae	**2**		**1**		**3**		**6**	

Table 1: Phytolyth totals for the Niobrara soil samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Tallgrass Prairie Preserve soil samples

Lab Number TG-	12		1		6		Total	
Keeled*	3	1.34	3	1.34	2	0.89	8	1.49
Conical or typical rondel*	6	2.69	9	4.03	11	4.93	26	4.85
Pyramidal*	1	0.44	0	0.00	2	0.89	3	0.55
Long wavy trapezoid*	4	1.79	7	3.13	8	3.58	19	3.54
Trapezoid bilobate/Stipa-type*	3	1.34	6	2.69	2	0.89	11	2.05
Panicoid bilobates*	30	13.45	57	25.56	83	37.21	170	31.71
Crosses*	3	1.34	4	1.79	9	4.03	16	2.98
Polylobates*	2	0.896861	3	1.345291	0	0.00	5	0.932836
Short saddles*	106	47.53	28	12.55	25	11.21	159	29.66
Aristida-type bilobates*	1	0.44	3	1.34	1	0.44	5	0.93
Plateau/ Long saddles	17	7.62	14	6.27	13	5.82	44	8.20
Horned towers/rondels	23	10.31	27	12.10	18	8.07	68	12.68
Other non-diagnostic	0	0.00	2	0.89	0	0	2	0.37
Total short cells	199	89.23	163	82.74	174	86.56	536	86.31
Elongates	10	4.48	14	6.27	13	5.82	37	6.90
Trichomes	4	1.79	4	1.79	5	2.24	13	2.42
Bulliforms	10	4.48	15	6.72	9	4.03	34	6.34
Undetermined	0	0.00	1	0.44	0	0.00	1	0.18
TOTAL GRASS	223	100.00	197	100.00	201	100.00	621	100.00
Pooideae	**17**		**25**		**25**		**67**	
Panicoideae	**35**		**64**		**92**		**191**	
Chloridoideae	**106**		**28**		**25**		**159**	
Aristidoideae	**1**		**3**		**1**		**5**	

Table 2: Phytolyth totals for the Tallgrass soil samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Sandsage Bison Range soil sample								
Lab Number FW-	1B		2A		1A		Total	
Keeled*	6	2.99	7	3.48	4	1.99	17	3.59
Conical or typical rondel*	9	4.48	6	2.99	12	5.97	27	5.70
Pyramidal*	2	1.00	4	1.99	1	0.50	7	1.48
Long wavy trapezoid*	11	5.47	7	3.48	8	3.98	26	5.49
Trapezoid bilobate/Stipa-type*	3	1.49	8	3.98	3	1.49	14	2.95
Panicoid bilobates*	9	4.48	13	6.47	10	4.98	32	6.75
Crosses*	2	1.00	3	1.49	4	1.99	9	1.90

Polylobates*	0	0.00	0	0.00	2	1.00	2	0.42
Short saddles*	68	33.83	95	47.26	73	36.32	236	49.79
Aristida-type bilobates*	3	1.49	2	1.00	5	2.49	10	2.11
Plateau/ Long saddles	22	10.95	11	5.47	14	6.97	47	9.92
Horned towers/rondels	16	7.96	12	5.97	18	8.96	46	9.70
Other non-diagnostic	1	0.50	0	0.00	0	0.00	1	0.21
Total short cells	152	75.62	168	81.55	154	76.24	474	100.00
Elongates	20	9.95	16	7.96	22	10.95	58	12.24
Trichomes	9	4.48	4	1.99	7	3.48	20	4.22
Bulliforms	20	9.95	18	8.96	19	9.45	57	12.03
Undetermined	0	0.00		0.00		0.00	0	0.00
TOTAL GRASS	201	100.00	206	100.00	202	100.00	609	128.48
Pooideae	**31**		**32**		**28**		**91**	
Panicoideae	**11**		**16**		**16**		**43**	
Chloridoideae	**68**		**95**		**73**		**236**	
Aristidoideae	**3**		**2**		**5**		**10**	

Table 3: Phytolyth totals for the Sandsage soil samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Lake Scott State Park soil samples						
Lab Number SC-	1		2		total	
Keeled*	3	1.41	6	2.94	9	2.16
Conical or typical rondel*	5	2.35	4	1.96	9	2.16
Pyramidal*	1	0.47	1	0.49	2	0.48
Long wavy trapezoid*	8	3.76	7	3.43	15	3.60
Trapezoid bilobate/Stipa-type*	3	1.41	8	3.92	11	2.64
Panicoid bilobates*	8	3.76	8	3.92	16	3.84
Crosses*	3	1.41	6	2.94	9	2.16
Polylobates*	1	0.47	1	0.49	2	0.48
Short saddles*	126	59.15	101	49.51	227	54.44
Aristida-type bilobates*	2	0.94	3	1.47	5	1.20
Plateau/ Long saddles	6	2.82	2	0.98	8	1.92
Horned towers/rondels	13	6.10	15	7.35	28	6.71
Other non-diagnostic	2	0.94	0	0.00	2	0.48
Total short cells	181	84.98	162	79.41	343	82.25
Elongates	12	5.63	14	6.86	26	6.24

Trichomes	3	1.41	4	1.96	7	1.68
Bulliforms	17	7.98	24	11.76	41	9.83
Undetermined	0	0.00	0	0.00	0	0.00
TOTAL GRASS	213	100.00	204	100.00	417	100.00
Pooideae	**20**		**26**		**46**	
Panicoideae	**11**		**14**		**25**	
Chloridoideae	**126**		**101**		**227**	
Aristidoideae	**2**		**3**		**5**	

Table 4: Phytolyth totals for the Lake Scott soil samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Niobrara Valley Preserve dental sample										
Lab Number R-	7		6		5		4		Total	
Keeled*	5	2.18	7	3.13	2	1.00	3	1.41	17	1.96
Conical or typical rondel*	7	3.06	12	5.36	6	2.99	10	4.69	35	4.04
Pyramidal*	0	0.00	2	0.89	0	0.00	2	0.94	4	0.46
Long wavy trapezoid*	0	0.00	2	0.89	2	1.00	2	0.94	6	0.69
Trapezoid bilobate/Stipa-type*	7	3.06	15	6.70	4	1.99	5	2.35	31	3.58
Panicoid bilobates*	104	45.41	47	20.98	26	12.94	56	26.29	233	26.87
Crosses*	16	6.99	15	6.70	11	5.47	19	8.92	61	7.04
Polylobates*	2	0.87	1	0.45	0	0.00	0	0.00	3	0.35
Short saddles*	48	20.96	55	24.55	74	36.82	59	27.70	236	27.22
Aristida-type bilobates*	7	3.06	1	0.45	1	0.50	3	1.41	12	1.38
Plateau/ Long saddles	22	9.61	26	11.61	38	18.91	23	10.80	109	12.57
Horned towers/rondels	7	3.06	22	9.82	28	13.93	10	4.69	67	7.73
Other non-diagnostic	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total short cells	225	98.25	205	91.52	192	95.52	192	90.14	814	93.89
Elongates	2	0.87	11	4.91	5	2.49	9	4.23	27	3.11
Trichomes	1	0.44	5	2.23	0	0.00	2	0.94	8	0.92
Bulliforms	1	0.44	3	1.34	4	1.99	10	4.69	18	2.08
Undetermined	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
TOTAL GRASS	**229**	100.00	224	100.00	201	100.00	213	100.00	867	100.00

Pooideae	**19**		**38**		**14**		**22**		**93**	
Panicoideae	**122**		**63**		**37**		**75**		**297**	
Chloridoideae	**48**		**55**		**74**		**59**		**236**	
Aristidoideae	**7**		**1**		**1**		**3**		**12**	

Table 5: Phytolyth totals for the Niobrara dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Tallgrass Prairie Preserve dental sample																
Lab Number R-	14		13		12		11		10		9		8		total	
Keeled*	2	0.99	2	2.27	5	2.55	2	2.22	1	1.41	7	3.11	0	0.00	19	2.17
Conical or typical rondel*	11	5.45	5	5.68	9	4.59	6	6.67	4	5.63	9	4.00	1	25.00	45	5.14
Pyramidal*	3	1.49	1	1.14	3	1.53	2	2.22	1	1.41	0	0.00	0	0.00	10	1.14
Long wavy trapezoid*	9	4.46	0	0.00	2	1.02	0	0.00	2	2.82	4	1.78	0	0.00	17	1.94
Trapezoid bilobate/Stipa-type*	6	2.97	2	2.27	4	2.04	1	1.11	1	1.41	8	3.56	0	0.00	22	2.51
Panicoid bilobates*	34	16.83	14	15.91	35	17.86	21	23.33	16	22.54	43	19.11	0	0.00	163	18.61
Crosses*	0	0.00	2	2.27	2	1.02	0	0.00	5	7.04	11	4.89	0	0.00	20	2.28
Polylobates*	1	0.50	0	0.00	2	1.02	0	0.00	0	0.00	1	0.44	0	0.00	4	0.46
Short saddles*	53	26.24	17	19.32	50	25.51	12	13.33	14	19.72	48	21.33	0	0.00	194	22.15
Aristida-type bilobates*	1	0.50	1	1.14	9	4.59	4	4.44	2	2.82	6	2.67	0	0.00	23	2.63
Plateau/ Long saddles	22	10.89	16	18.18	26	13.27	17	18.89	11	15.49	42	18.67	1	25.00	135	15.41
Horned towers/rondels	18	8.91	10	11.36	18	9.18	6	6.67	2	2.82	20	8.89	0	0.00	74	8.45
Other non-diagnostic	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total short cells	160	79.21	70	79.55	165	84.18	71	78.89	59	83.10	199	88.44	2	50.00	726	82.88
Elongates	25	12.38	12	13.64	23	11.73	8	8.89	7	9.86	18	8.00	1	25.00	94	10.73
Trichomes	5	2.48	0	0.00	0	0.00	5	5.56	2	2.82	4	1.78	1	25.00	17	1.94
Bulliforms	12	5.94	6	6.82	8	4.08	6	6.67	3	4.23	4	1.78	0	0.00	39	4.45
Undetermined	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00

TOTAL GRASS	202	100.00	88	100.00	196	100.00	90	100.00	71	100.00	225	100.00	4	100.00	876	100.00
Pooideae	**31**		**10**		**23**		**11**		**9**		**28**		**1**		**113**	
Panicoideae	**35**		**16**		**39**		**21**		**21**		**55**		**0**		**187**	
Chloridoideae	**53**		**17**		**50**		**12**		**14**		**48**		**0**		**194**	
Aristidoideae	**1**		**1**		**9**		**4**		**2**		**6**		**0**		**23**	

Table 6: Phytolyth totals for the Tallgrass dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Sandsage Bison Range dental sample						
Lab Number R-	16		15		Total	
Keeled*	2	0.97	3	2.33	5	1.49
Conical or typical rondel*	9	4.37	7	5.43	16	4.78
Pyramidal*	3	1.46	2	1.55	5	1.49
Long wavy trapezoid*	5	2.43	4	3.10	9	2.69
Trapezoid bilobate/Stipa-type*	4	1.94	3	2.33	7	2.09
Panicoid bilobates*	14	6.80	5	3.88	19	5.67
Crosses*	3	1.46	2	1.55	5	1.49
Polylobates*	0	0.00	1	0.78	1	0.30
Short saddles*	62	30.10	35	27.13	97	28.96
Aristida-type bilobates*	0	0.00	2	1.55	2	0.60
Plateau/ Long saddles	41	19.90	17	13.18	58	17.31
Horned towers/rondels	15	7.28	19	14.73	34	10.15
Other non-diagnostic	0	0.00	0	0.00	0	0.00
Total short cells	158	76.70	100	77.52	258	77.01
Elongates	25	12.14	17	13.18	42	12.54
Trichomes	5	2.43	3	2.33	8	2.39
Bulliforms	18	8.74	9	6.98	27	8.06
Undetermined	0	0.00	0	0.00	0	0.00
TOTAL GRASS	206	100.00	129	100.00	335	100.00
Pooideae	**23**		**19**		**42**	
Panicoideae	**17**		**8**		**25**	
Chloridoideae	**62**		**35**		**97**	

Aristidoideae	**0**		**2**		**2**	

Table 7: Phytolyth totals for the Sandsage dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Folsom dental sample												
Lab Number FM-	7		6		5		4		3		total	
Keeled*	0	0.00	0	0.00	0	0.00	1	3.85	0	0.00	1	1.06
Conical or typical rondel*	3	9.09	0	0.00	2	20.00	4	15.38	3	15.00	12	12.77
Pyramidal*	3	9.09	0	0.00	0	0.00	3	11.54	1	5.00	7	7.45
Long wavy trapezoid*	2	6.06	0	0.00	0	0.00	1	3.85	0	0.00	3	3.19
Trapezoid bilobate/Stipa-type*	2	6.06	0	0.00	1	10.00	0	0.00	0	0.00	3	3.19
Panicoid bilobates*	2	6.06	0	0.00	0	0.00	2	7.69	2	10.00	6	6.38
Crosses*	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Polylobates*	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Short saddles*	3	9.09	0	0.00	1	10.00	3	11.54	2	10.00	9	9.57
Aristida-type bilobates*	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Plateau/ Long saddles	5	15.15	1	20.00	1	10.00	3	11.54	3	15.00	13	13.83
Horned towers/rondels	1	3.03	1	20.00	1	10.00	0	0.00	2	10.00	5	5.32
Other non-diagnostic	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total short cells	21	63.64	2	40.00	6	60.00	17	65.38	13	65.00	59	62.77
Elongates	6	18.18	2	40.00	2	20.00	4	15.38	2	10.00	16	17.02
Trichomes	3	9.09	0	0.00	0	0.00	0	0.00	1	5.00	4	4.26
Bulliforms	3	9.09	1	20.00	2	20.00	5	19.23	4	20.00	15	15.96
Undetermined	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
TOTAL GRASS	33	100.00	5	100.00	10	100.00	26	100.00	20	100.00	94	100.00
Pooideae	**10**		**0**		**3**		**9**		**4**		**26**	
Panicoideae	**2**		**0**		**0**		**2**		**2**		**6**	
Chloridoideae	**3**		**0**		**1**		**3**		**2**		**9**	
Aristidoideae	**0**		**0**		**0**		**0**		**0**		**0**	

Table 8: Phytolyth totals for the Folsom dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Cooper dental samples																
Lab Number R-	23		22		21		20		19		18		17		total	
Keeled*	0	0.00	0	0.00	2	2.47	0	0.00	0	0.00	0	0.00	1	3.13	3	1.05
Conical or typical rondel*	3	14.29	4	7.84	4	4.94	5	8.33	1	3.57	2	14.29	1	3.13	20	6.97
Pyramidal*	0	0.00	0	0.00	1	1.23	1	1.67	0	0.00	0	0.00	1	3.13	3	1.05
Long wavy trapezoid*	1	4.76	6	11.76	2	2.47	3	5.00	2	7.14	0	0.00	1	3.13	15	5.23
Trapezoid bilobate/Stipa-type*	1	4.76	0	0.00	1	1.23	1	1.67	1	3.57	1	7.14	0	0.00	5	1.74
Panicoid bilobates*	3	14.29	5	9.80	5	6.17	3	5.00	0	0.00	0	0.00	2	6.25	18	6.27
Crosses*	1	4.76	0	0.00	1	1.23	0	0.00	0	0.00	0	0.00	0	0.00	2	0.70
Polylobates*	0	0.00	0	0.00	0	0.00	1	1.67	0	0.00	0	0.00	1	3.13	2	0.70
Short saddles*	0	0.00	12	23.53	30	37.04	17	28.33	10	35.71	0	0.00	4	12.50	73	25.44
Aristida-type bilobates*	0	0.00	0	0.00	2	2.47	0	0.00	0	0.00	0	0.00	1	3.13	3	1.05
Plateau/ Long saddles	2	9.52	3	5.88	14	17.28	9	15.00	4	14.29	2	14.29	4	12.50	38	13.24
Horned towers/rondels	3	14.29	2	3.92	3	3.70	4	6.67	3	10.71	2	14.29	4	12.50	21	7.32
Other non-diagnostic	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total short cells	14	66.67	32	62.75	65	80.25	44	73.33	21	75.00	7	50.00	20	62.50	203	70.73
Elongates	4	19.05	12	23.53	9	11.11	9	15.00	2	7.14	5	35.71	7	21.88	48	16.72
Trichomes	1	4.76	3	5.88	4	4.94	2	3.33	2	7.14	0	0.00	2	6.25	14	4.88
Bulliforms	2	9.52	4	7.84	3	3.70	5	8.33	3	10.71	2	14.29	3	9.38	22	7.67
Undetermined	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
TOTAL GRASS	21	100.00	51	100.00	81	100.00	60	100.00	28	100.00	14	100.00	32	100.00	287	100.00
Pooideae	**5**		**10**		**10**		**10**		**4**		**3**		**4**		**46**	
Panicoideae	**4**		**5**		**6**		**4**		**0**		**0**		**3**		**22**	
Chloridoideae	**0**		**12**		**30**		**17**		**10**		**0**		**4**		**73**	

Aristidoideae	**0**		**0**		**2**		**0**		**0**		**0**		**1**		**3**	

Table 9: Phytolyth totals for the Cooper dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Ravenscroft II dental samples												
Lab Number R-	28		27		26		25		24		total	
Keeled*	0	0.00	1	8.33	0	0.00	0	0.00	0	0.00	1	1.12
Conical or typical rondel*	3	18.75	3	25.00	0	0.00	2	5.71	2	10.53	10	11.24
Pyramidal*	0	0.00	0	0.00	0	0.00	2	5.71	0	0.00	2	2.25
Long wavy trapezoid*	2	12.50	1	8.33	1	14.29	3	8.57	2	10.53	9	10.11
Trapezoid bilobate/Stipa-type*	1	6.25	0	0.00	0	0.00	3	8.57	0	0.00	4	4.49
Panicoid bilobates*	0	0.00	0	0.00	0	0.00	2	5.71	1	5.26	3	3.37
Crosses*	0	0.00	0	0.00	0	0.00	0	0.00	1	5.26	1	1.12
Polylobates*	1	6.25	0	0.00	0	0.00	0	0.00	0	0.00	1	1.12
Short saddles*	2	12.50	0	0.00	1	14.29	4	11.43	3	15.79	10	11.24
Aristida-type bilobates*	0	0.00	0	0.00	0	0.00	2	5.71	0	0.00	2	2.25
Plateau/ Long saddles	1	6.25	0	0.00	0	0.00	1	2.86	1	5.26	3	3.37
Horned towers/rondels	0	0.00	2	16.67	2	28.57	3	8.57	1	5.26	8	8.99
Other non-diagnostic	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total short cells	10	62.50	7	58.33	4	57.14	22	62.86	11	57.89	54	60.67
Elongates	2	12.50	2	16.67	0	0.00	4	11.43	4	21.05	12	13.48
Trichomes	2	12.50	0	0.00	1	14.29	4	11.43	2	10.53	9	10.11
Bulliforms	2	12.50	3	25.00	2	28.57	5	14.29	2	10.53	14	15.73
Undetermined	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
TOTAL GRASS	16	100.00	12	100.00	7	100.00	35	100.00	19	100.00	89	100.00
Pooideae	**6**		**5**		**1**		**10**		**4**		**26**	
Panicoideae	**1**		**0**		**0**		**2**		**2**		**5**	
Chloridoideae	**2**		**0**		**1**		**4**		**3**		**10**	
Aristidoideae	**0**		**0**		**0**		**2**		**0**		**2**	

Table 10: Phytolyth totals for the Ravenscroft II dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Badger Hole dental Samples						
Lab Number R-	32		31		total	
Keeled*	0	0.00	1	1.75	1	1.47
Conical or typical rondel*	0	0.00	4	7.02	4	5.88
Pyramidal*	0	0.00	0	0.00	0	0.00
Long wavy trapezoid*	0	0.00	5	8.77	5	7.35
Trapezoid bilobate/Stipa-type*	0	0.00	3	5.26	3	4.41
Panicoid bilobates*	1	9.09	5	8.77	6	8.82
Crosses*	1	9.09	0	0.00	1	1.47
Polylobates*	0	0.00	0	0.00	0	0.00
Short saddles*	0	0.00	10	17.54	10	14.71
Aristida-type bilobates*	0	0.00	1	1.75	1	1.47
Plateau/ Long saddles	2	18.18	7	12.28	9	13.24
Horned towers/rondels	1	9.09	5	8.77	6	8.82
Other non-diagnostic	0	0.00	0	0.00	0	0.00
Total short cells	5	45.45	41	71.93	46	67.65
Elongates	1	9.09	8	14.04	9	13.24
Trichomes	3	27.27	2	3.51	5	7.35
Bulliforms	2	18.18	6	10.53	8	11.76
Undetermined	0	0.00	0	0.00	0	0.00
TOTAL GRASS	11	100.00	57	100.00	68	100.00
Pooideae	**0**		**13**		**13**	
Panicoideae	**2**		**5**		**7**	
Chloridoideae	**0**		**10**		**10**	
Aristidoideae	**0**		**1**		**1**	

Table 11: Phytolyth totals for the Badger Hole dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Jake Bluff Dental sample										
Lab Number R-	34		33		30		29		total	
Keeled*	0	0.00	0	0.00	0	0.00	1	16.67	1	1.79
Conical or typical rondel*	1	14.29	0	0.00	0	0.00	1	16.67	2	3.57
Pyramidal*	0	0.00	1	3.70	1	6.25	0	0.00	2	3.57
Long wavy trapezoid*	0	0.00	2	7.41	0	0.00	0	0.00	2	3.57
Trapezoid bilobate/Stipa-type*	0	0.00	1	3.70	1	6.25	0	0.00	2	3.57
Panicoid bilobates*	0	0.00	2	7.41	1	6.25	0	0.00	3	5.36
Crosses*	0	0.00	0	0.00	1	6.25	0	0.00	1	1.79
Polylobates*	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Short saddles*	1	14.29	1	3.70	3	18.75	1	16.67	6	10.71
Aristida-type bilobates*	0	0.00	2	7.41	1	6.25	0	0.00	3	5.36
Plateau/ Long saddles	3	42.86	0	0.00	2	12.50	1	16.67	6	10.71
Horned towers/rondels	0	0.00	1	3.70	0	0.00	0	0.00	1	1.79
Other non-diagnostic	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
Total short cells	5	71.43	10	37.04	10	62.50	4	66.67	29	51.79
Elongates	1	14.29	9	33.33	4	25.00	2	33.33	16	28.57
Trichomes	0	0.00	3	11.11	1	6.25	0	0.00	4	7.14
Bulliforms	1	14.29	5	18.52	1	6.25	0	0.00	7	12.50
Undetermined	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
TOTAL GRASS	7	100.00	27	100.00	16	100.00	6	100.00	56	100.00
Pooideae	**1**		**4**		**2**		**2**		**9**	
Panicoideae	**0**		**2**		**2**		**0**		**4**	
Chloridoideae	**1**		**1**		**3**		**1**		**6**	
Aristidoideae	**0**		**2**		**1**		**0**		**3**	

Table 12: Phytolyth totals for the Jake Bluff dental samples. First value denotes phytolith total, second is the percentage values under Sample Number. * denotes diagnostic phytolith morphotype.

Graphs of identifiable phytolith morphotype percentages:

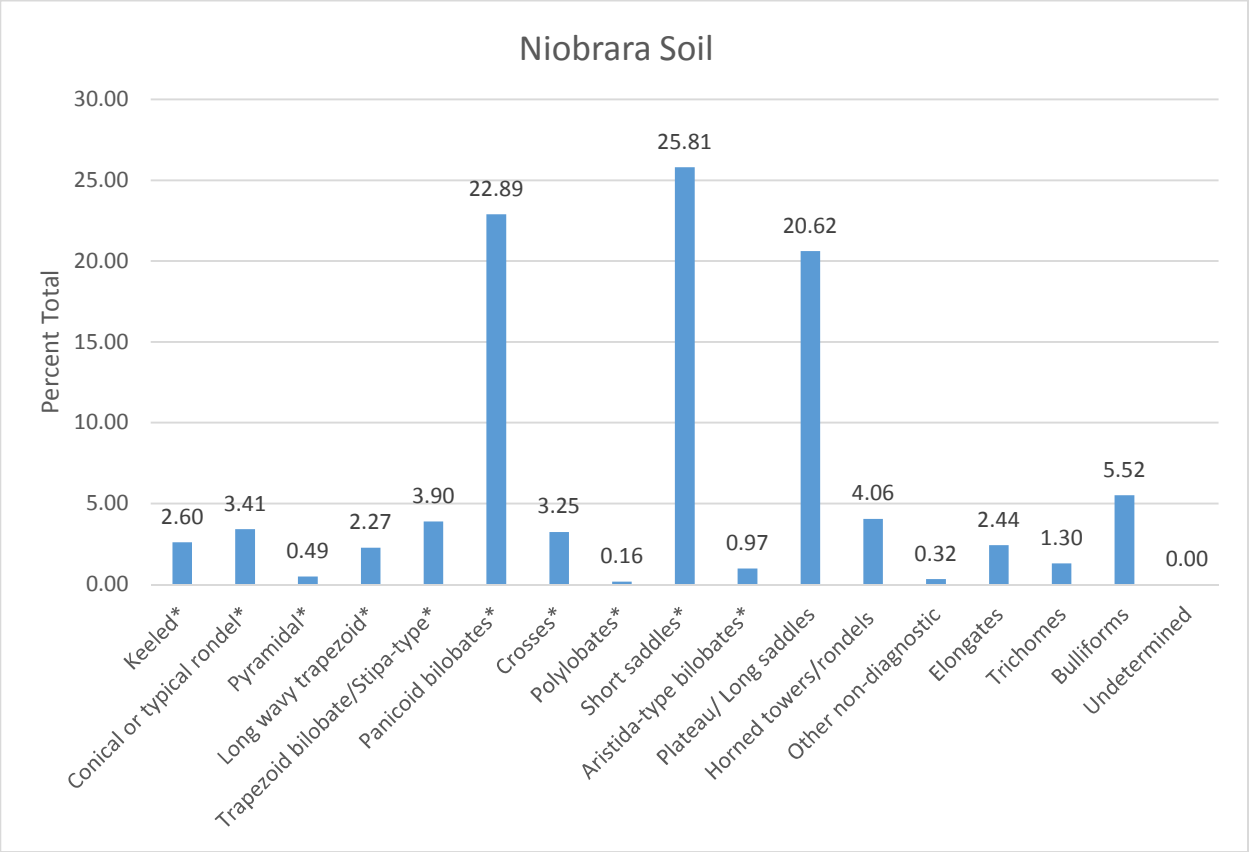

Figure 1. Niobrara Soil percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

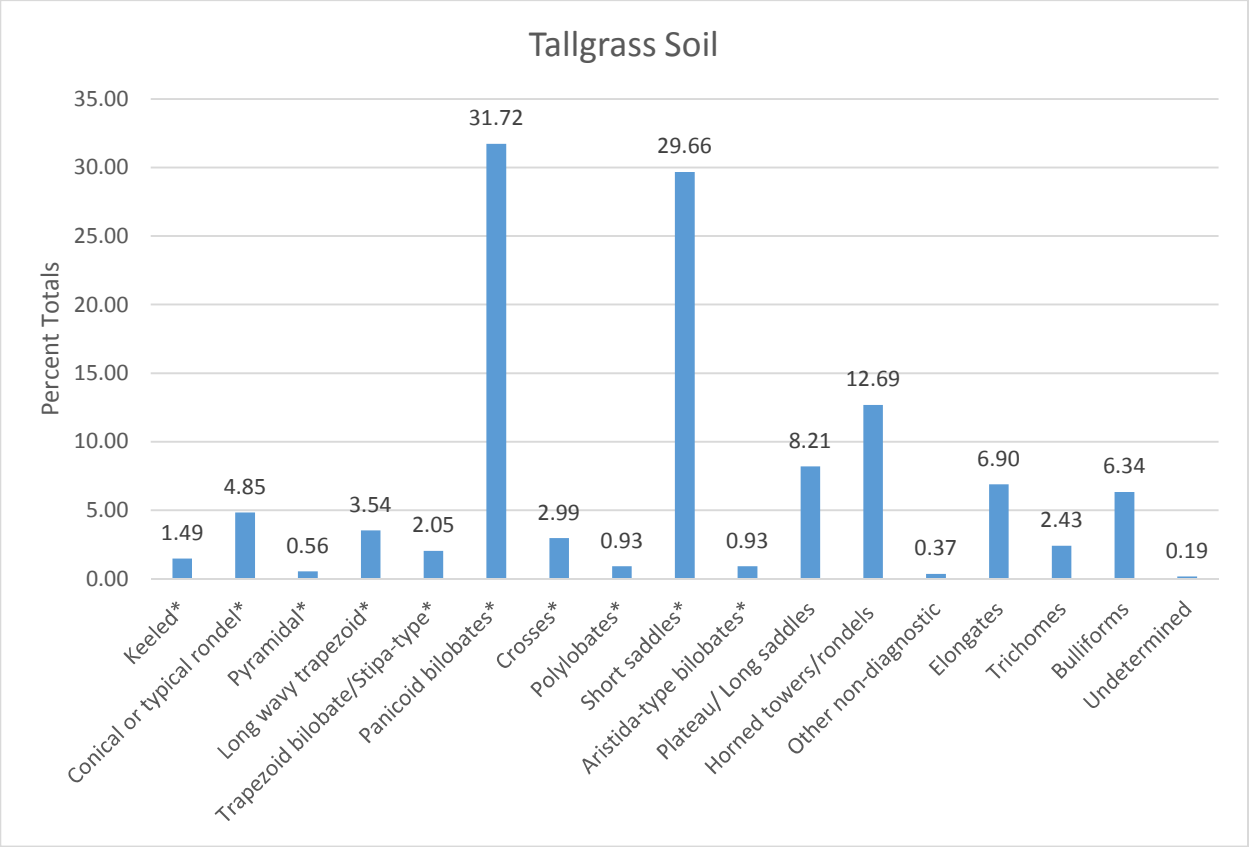

Figure 2. Tallgrass Soil percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

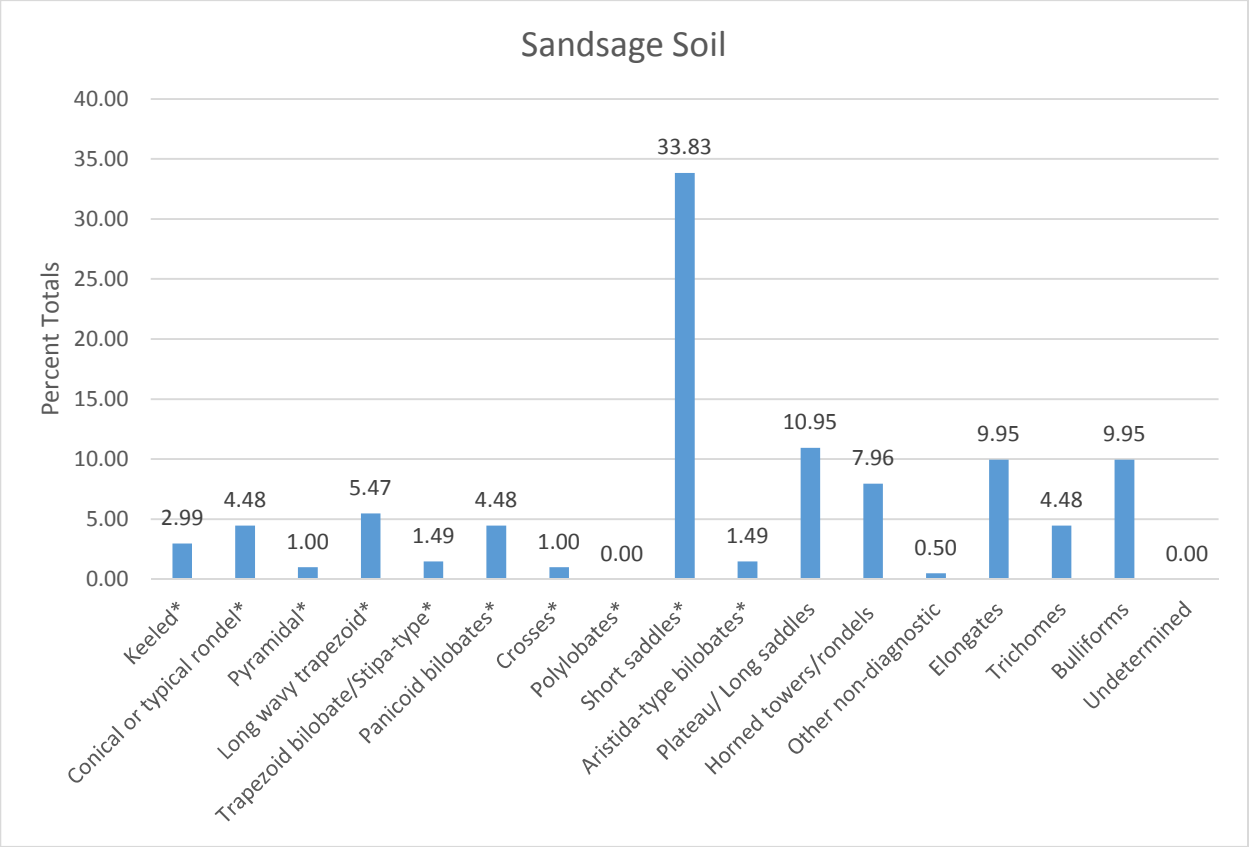

Figure 3. Sandsage Soil percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

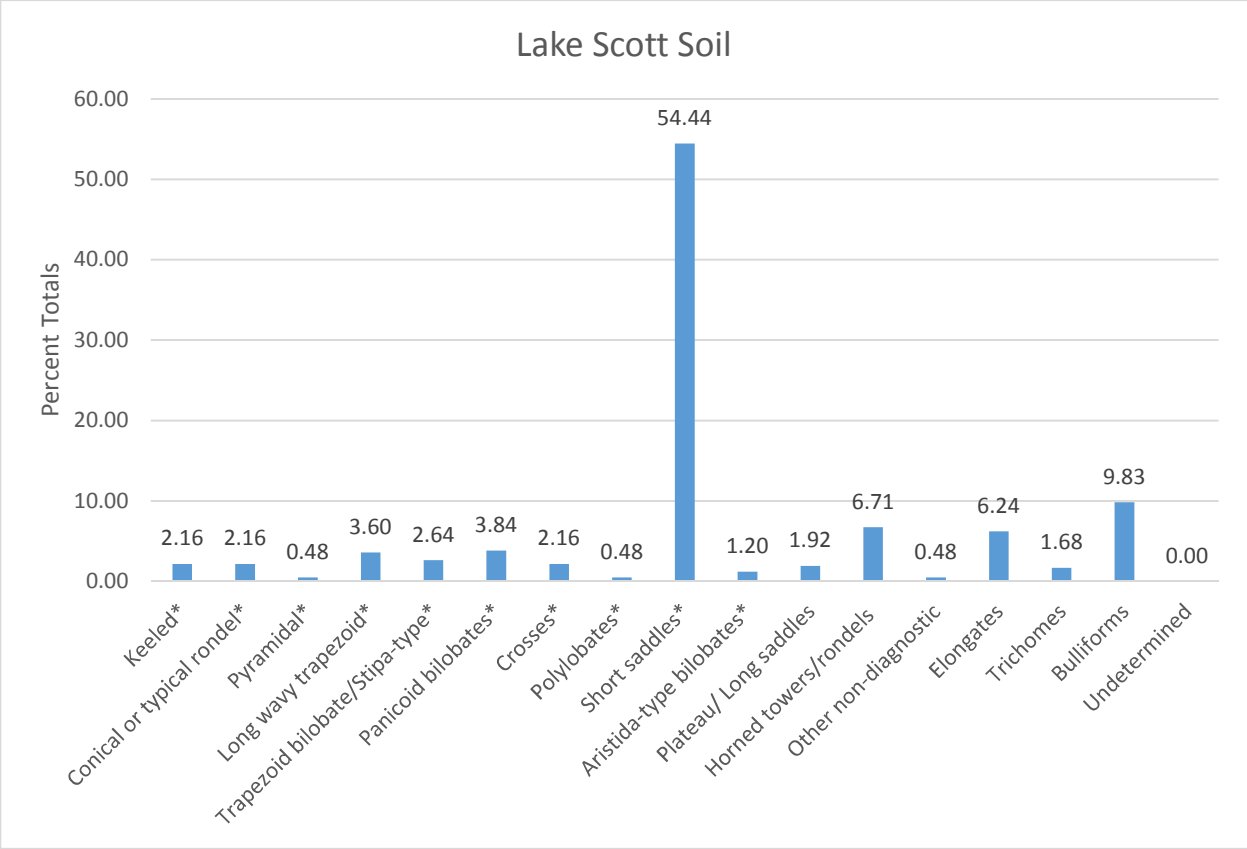

Figure 4. Lake Scott Soil percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

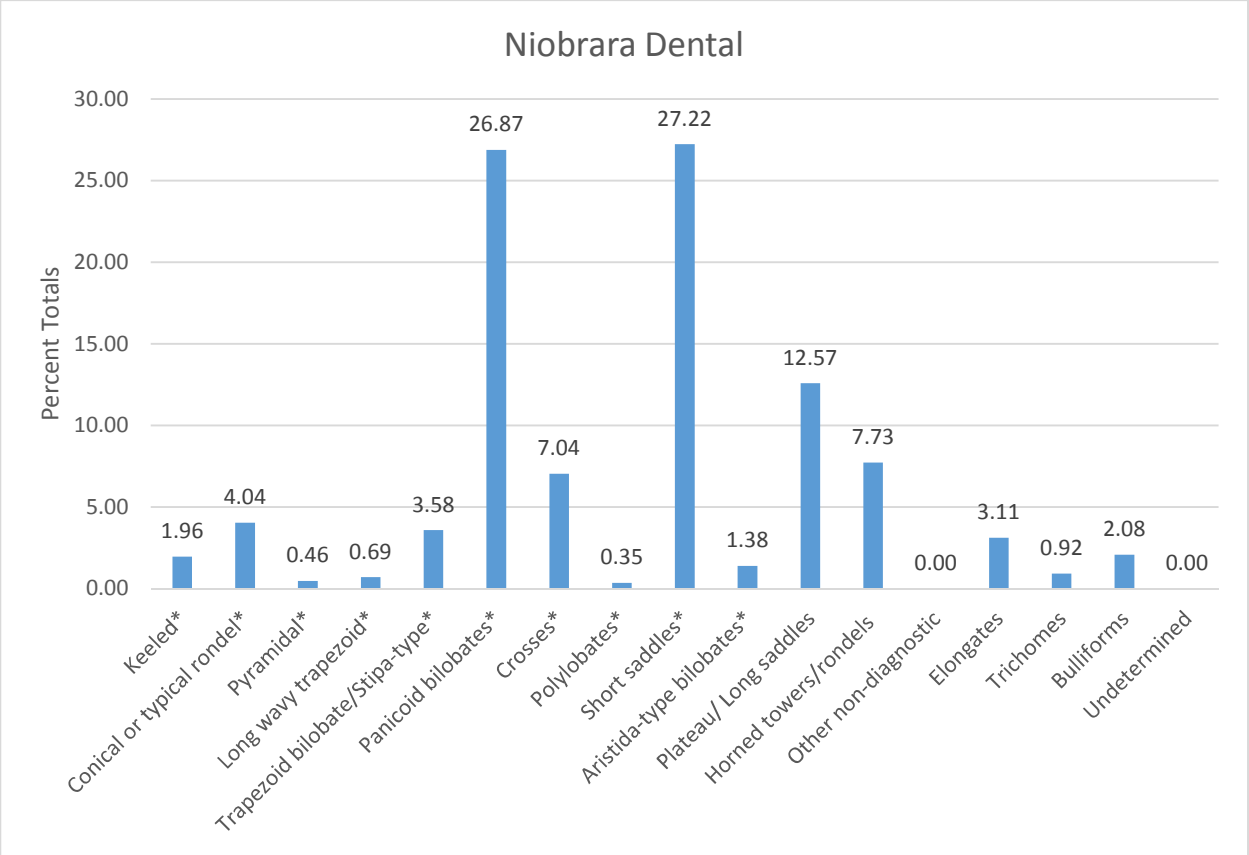

Figure 5. Niobrara Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

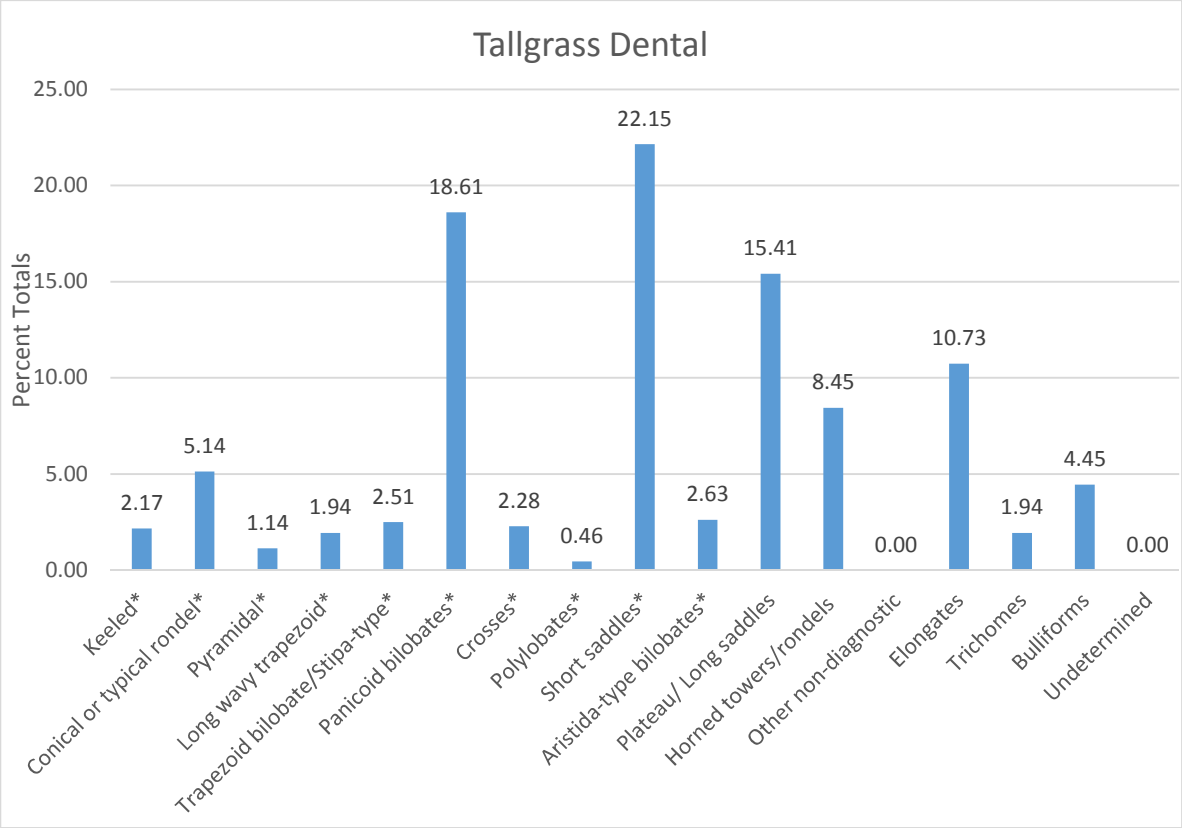

Figure 6. Tallgrass Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

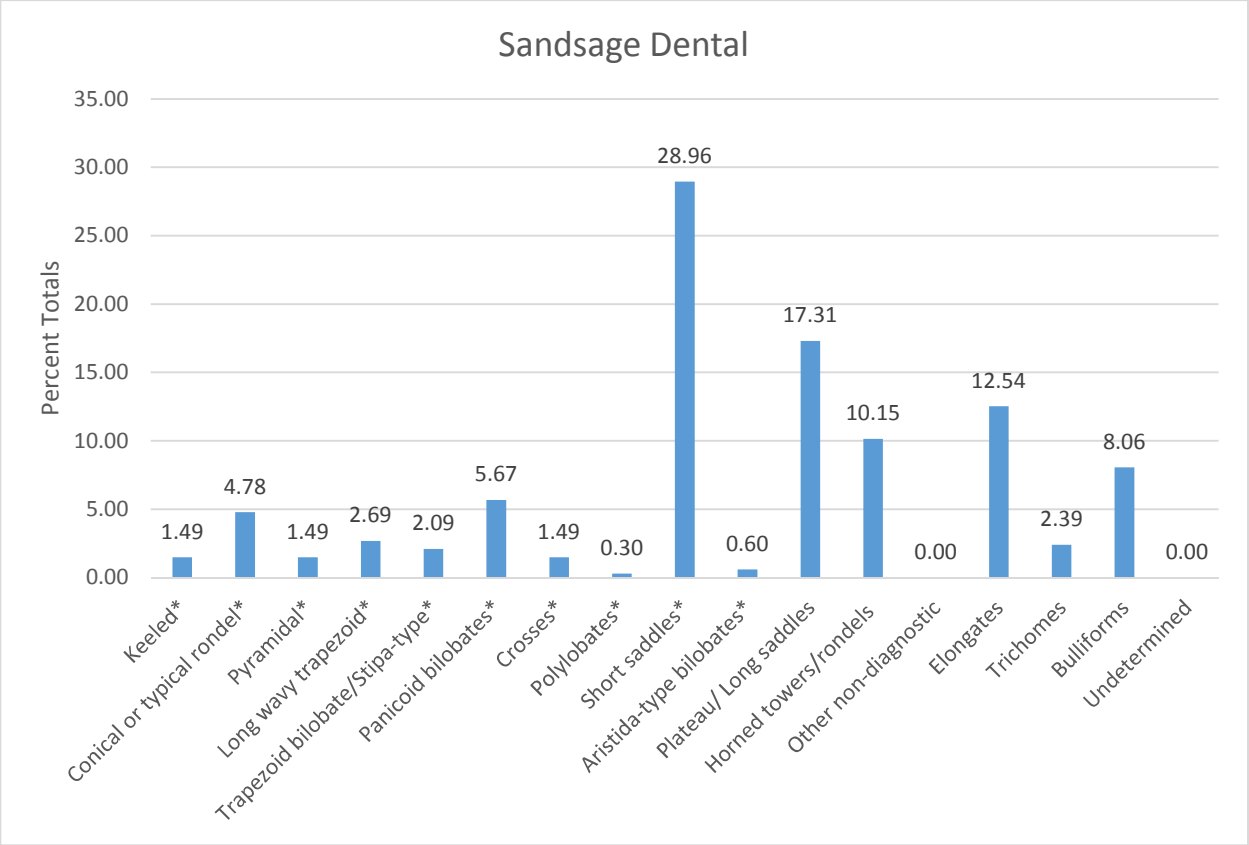

Figure 7. Sandsage Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

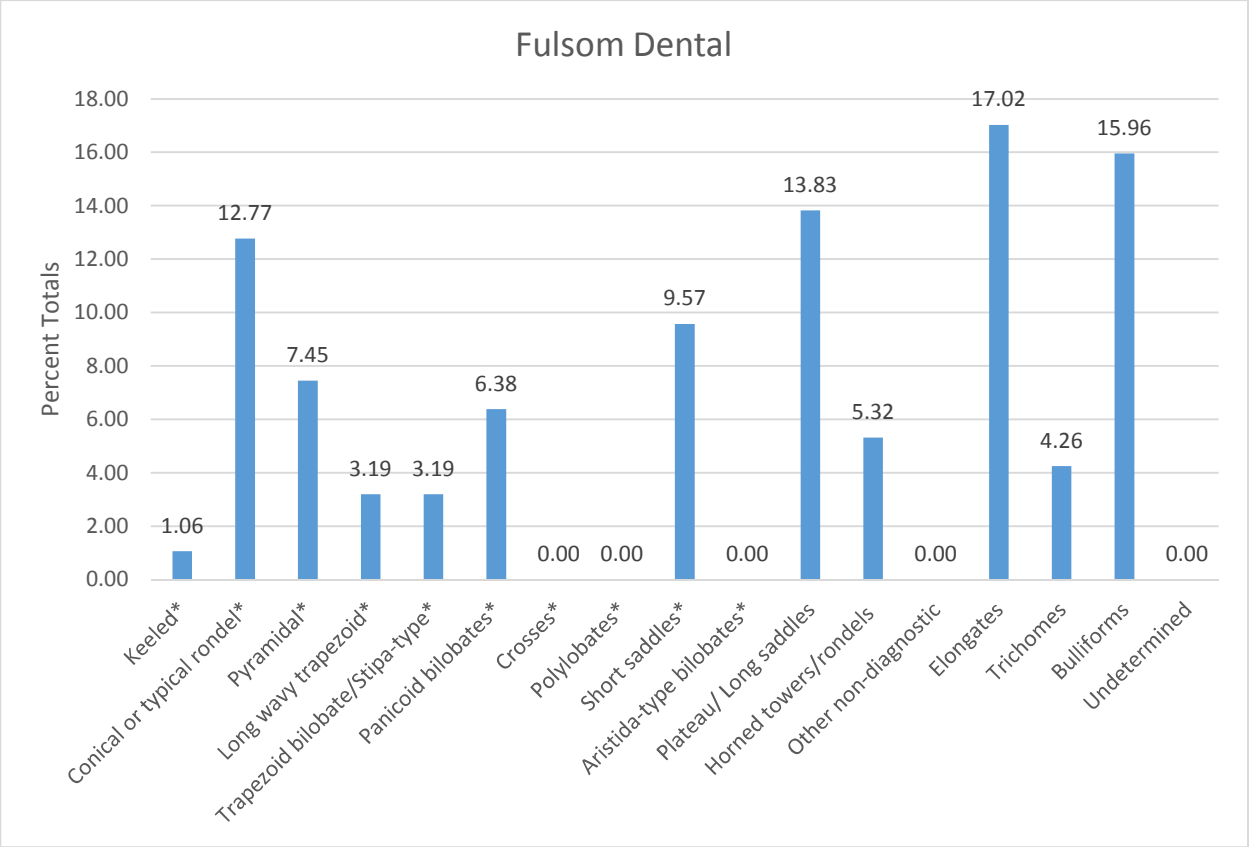

Figure 8. Folsom Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

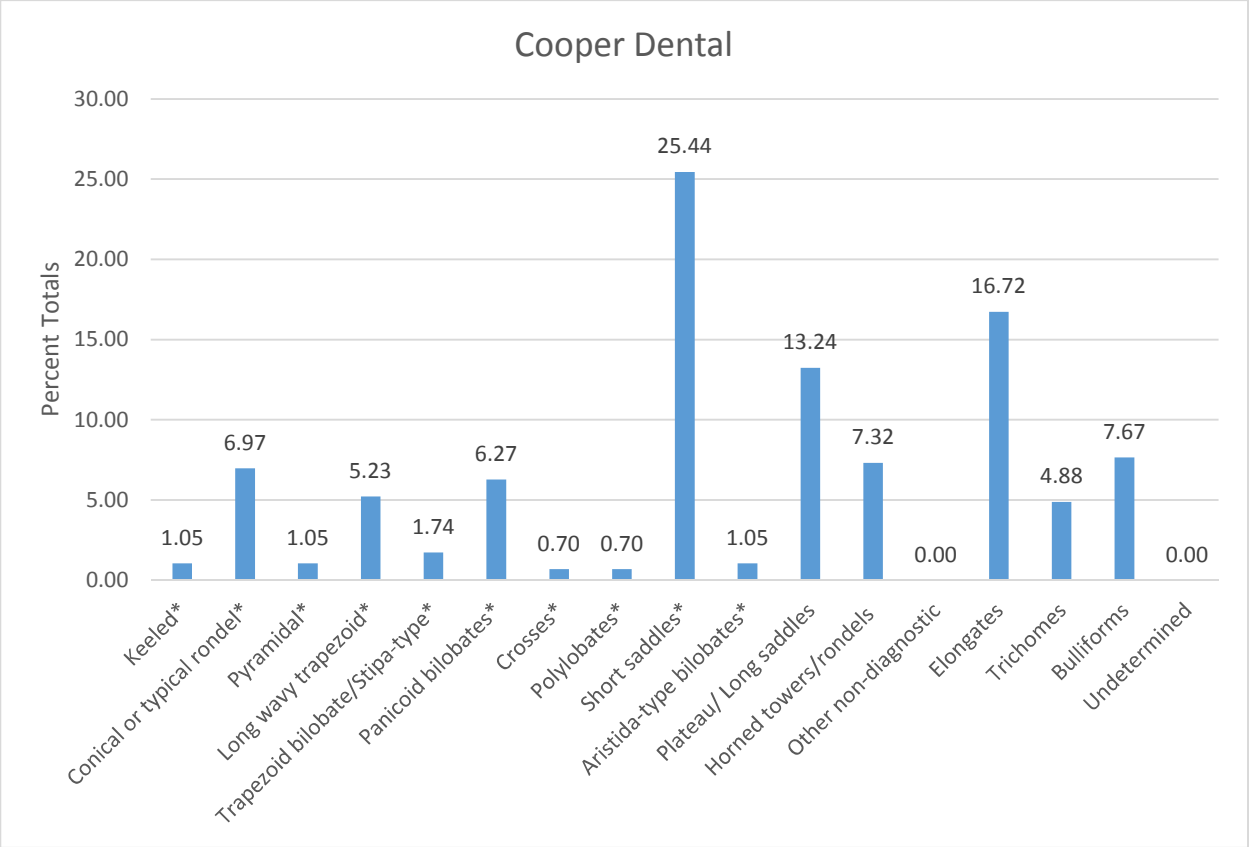

Figure 9. Cooper Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

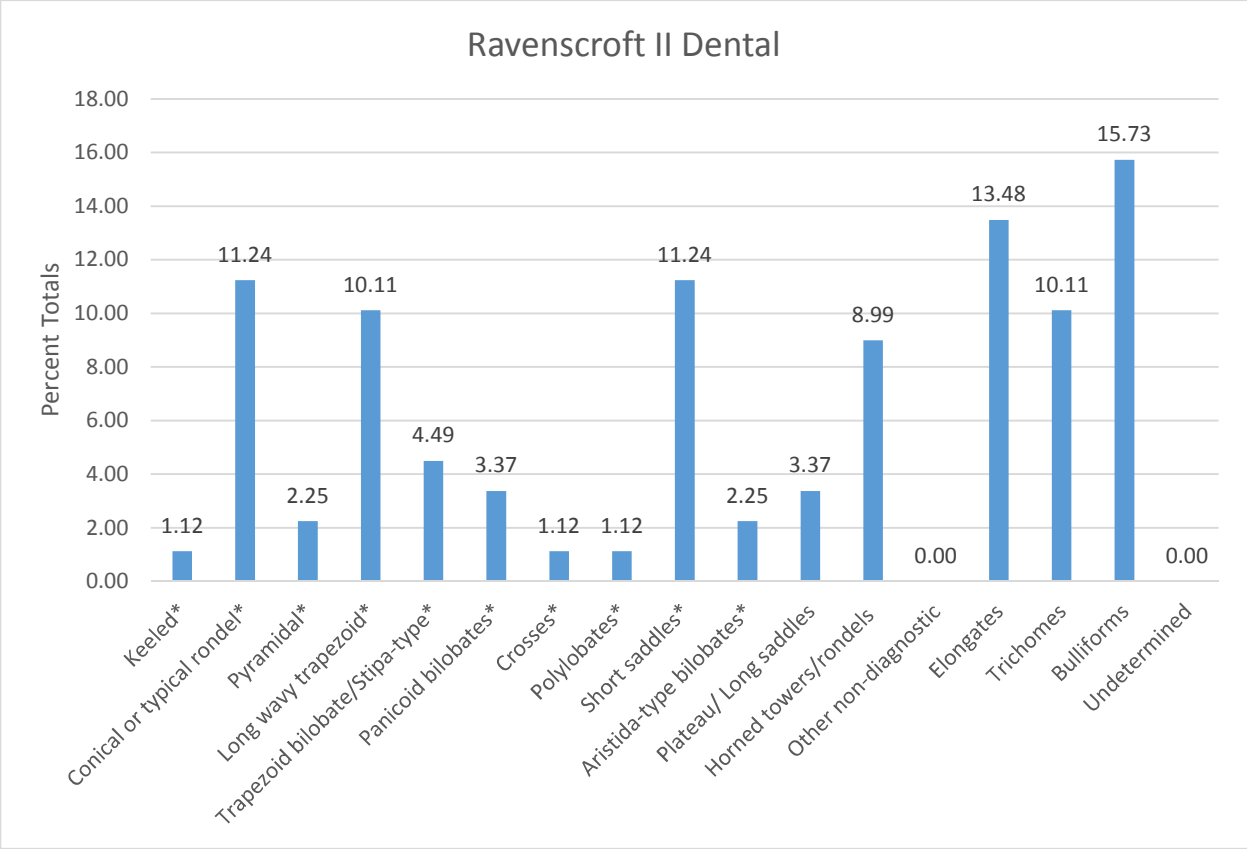

Figure 10. Ravenscroft II Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

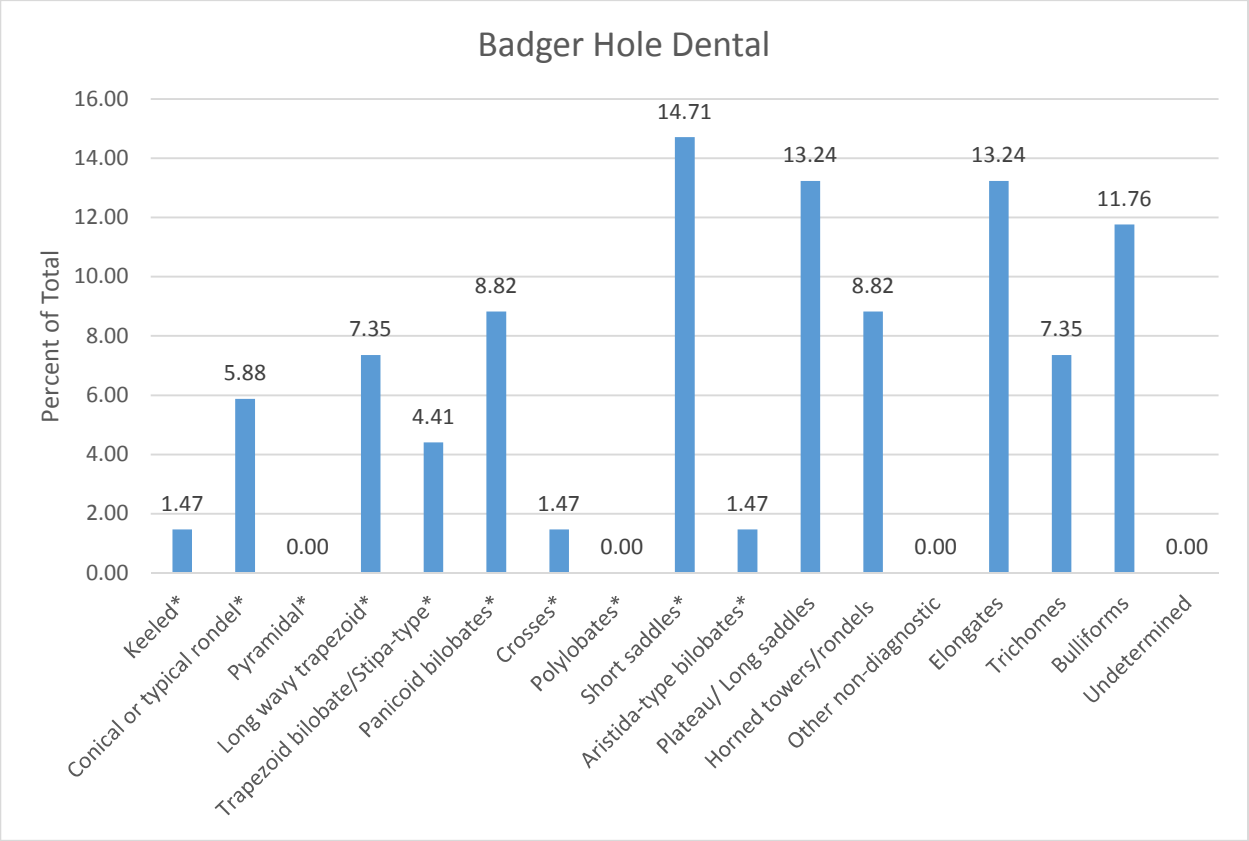

Figure 11. Badger Hole Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

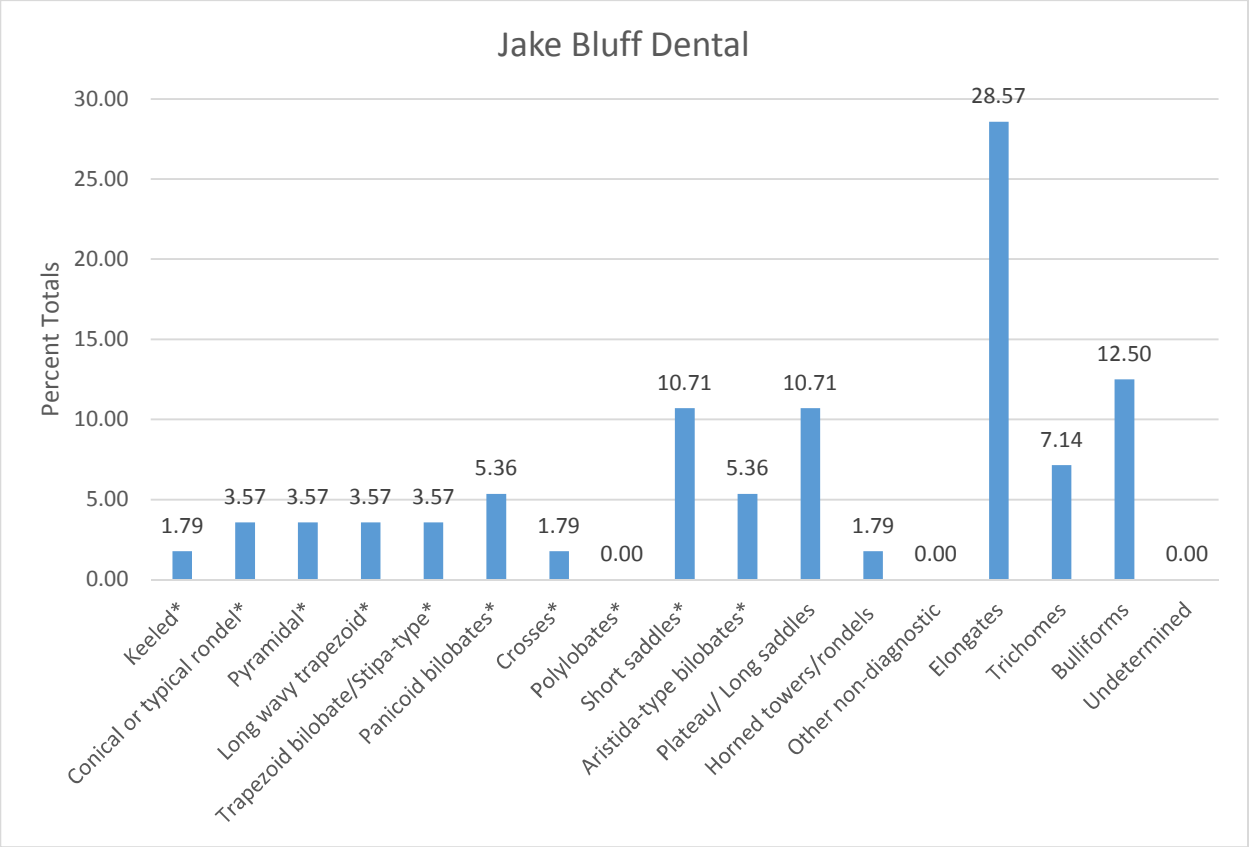

Figure 12. Jake Bluff Dental percent phytolith totals graph. * denotes diagnostic phytolith morphotype.

Clustering based on phytolith totals:

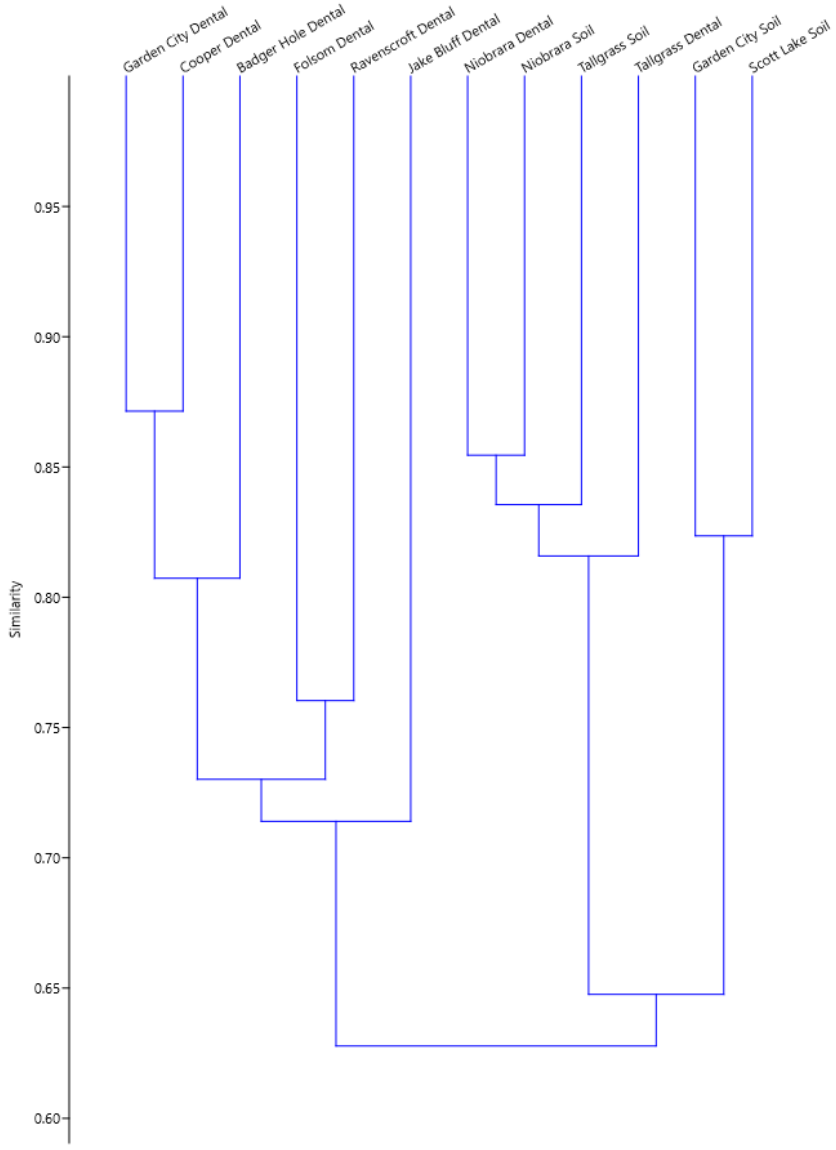

Figure 13. Bray-Curtis Clustering based on all phytoliths not only diagnostic morphotypes.

VITA

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